TWO DEVONIAN MITRATES FROM SOUTH AFRICA

by M. RUTA *and* J. N. THERON

ABSTRACT. The anomalocystitid mitrate *Placocystella africana* (Gydo and Voorstehoek shales, upper Emsian–lower Eifelian, Bokkeveld Group, Cape Province, South Africa) is redescribed. The internal anatomy of the head, the tail morphology and part of the nervous system are reconstructed for the first time. *P. africana* belongs to the family Allanicytidiidae, together with four other Silurian and Devonian species from Gondwana. The monophyly of the Allanicytidiidae is supported by cladistic analysis. A second mitrate from the upper Emsian of the Bokkeveld Group, *Bokkeveldia oosthuizeni* gen. et sp. nov. from the Gydo Shale, is described. The distinctive ventral head skeleton of this mitrate consists of 22 plates arranged in five transverse rows and is used as a reference to establish plate homologies in the anomalocystitids.

THE mitrates are calcite-plated deuterostomes of Ordovician to Carboniferous age. In most classifications, these fossils are regarded as echinoderms and are placed in the order Mitrata of the class Stylophora (Ubaghs 1967). All mitrates consist of a massive part, the head or theca, and an articulated appendage, the tail or aulacophore. No signs of radial symmetry are known in mitrates, but whether this is a primitive or derived feature is disputed.

The anatomy, orientation and systematic position of mitrates are strongly debated. Three schools of thought interpret these fossils in different ways. These different interpretations are referred to in the literature as the aulacophore theory of Ubaghs (1967 et seq.), the calcichordate theory of Jefferies (1967 et seq.) and the stele theory of Philip (1979, 1981). Reviews of these theories are found in Philip (1979), Chauvel (1981), Ubaghs (1981), Jollie (1982), Kolata and Jollie (1982), Jefferies (1986), Cripps (1991), Kolata *et al.* (1991) and especially Peterson (1994, 1995), who has recently criticized the calcichordate theory of Jefferies by testing its predictions in the context of a higher level phylogeny of the deuterostomes.

Two groups of mitrates, the Mitrocystitida and the Anomalocystitida (Caster 1952), deserve particular attention, since for Jefferies (1986, 1991), whose calcichordate theory is largely followed here, the mitrocystitid and anomalocystitid mitrates are stem-group craniates (see also Jefferies and Lewis 1978; Craske and Jefferies 1989; Cripps 1990; Beisswenger 1994). The mitrocystitids and the anomalocystitids would share with craniates a lateral line system and dorsal, touch-sensory branches of the trigeminal nerves (Jefferies 1986).

The mitrocystitids are likely to represent a paraphyletic group (Craske and Jefferies 1989). The monophyletic Anomalocystitida are characterized mainly by the possession of two articulated spines and by a regular arrangement of the head plates. The anomalocystitids from the Southern Hemisphere are of special interest, since most of them are comparatively less well known than the boreal species and no transitional forms are known that bridge the morphological gap between these two groups (but see Haude 1995).

In his extensive revision of the fossil faunas from the Bokkeveld Group of South Africa, Reed (1925) described a poorly preserved mitrate collected near Buffelskraal (Cape Province) and named it *Placocystis africanus*. This was the first mitrate recorded from the Southern Hemisphere. However, the choice of both the generic and the specific name was unfortunate, as *Placocystis* is an invalid emendation of *Placocystites* de Koninck (Bather 1900) and also a junior synonym of *Enoploura* Wetherby (Haeckel 1896). Furthermore, *Placocystis* is a feminine noun, whereas the adjective *africanus* is masculine. In 1936, Rennie described the mitrate *Placocystella capensis* on the

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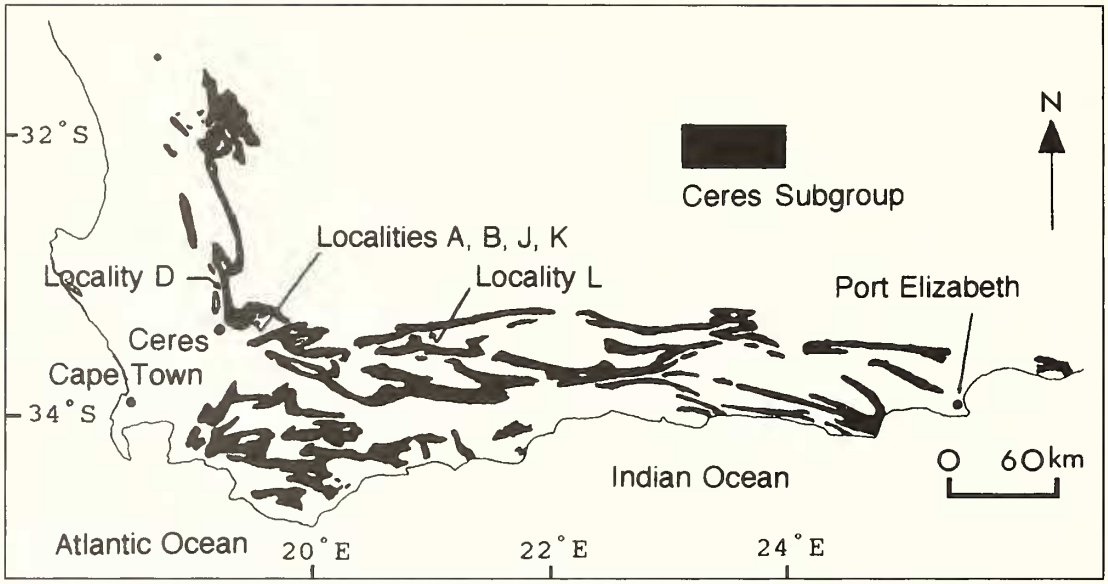


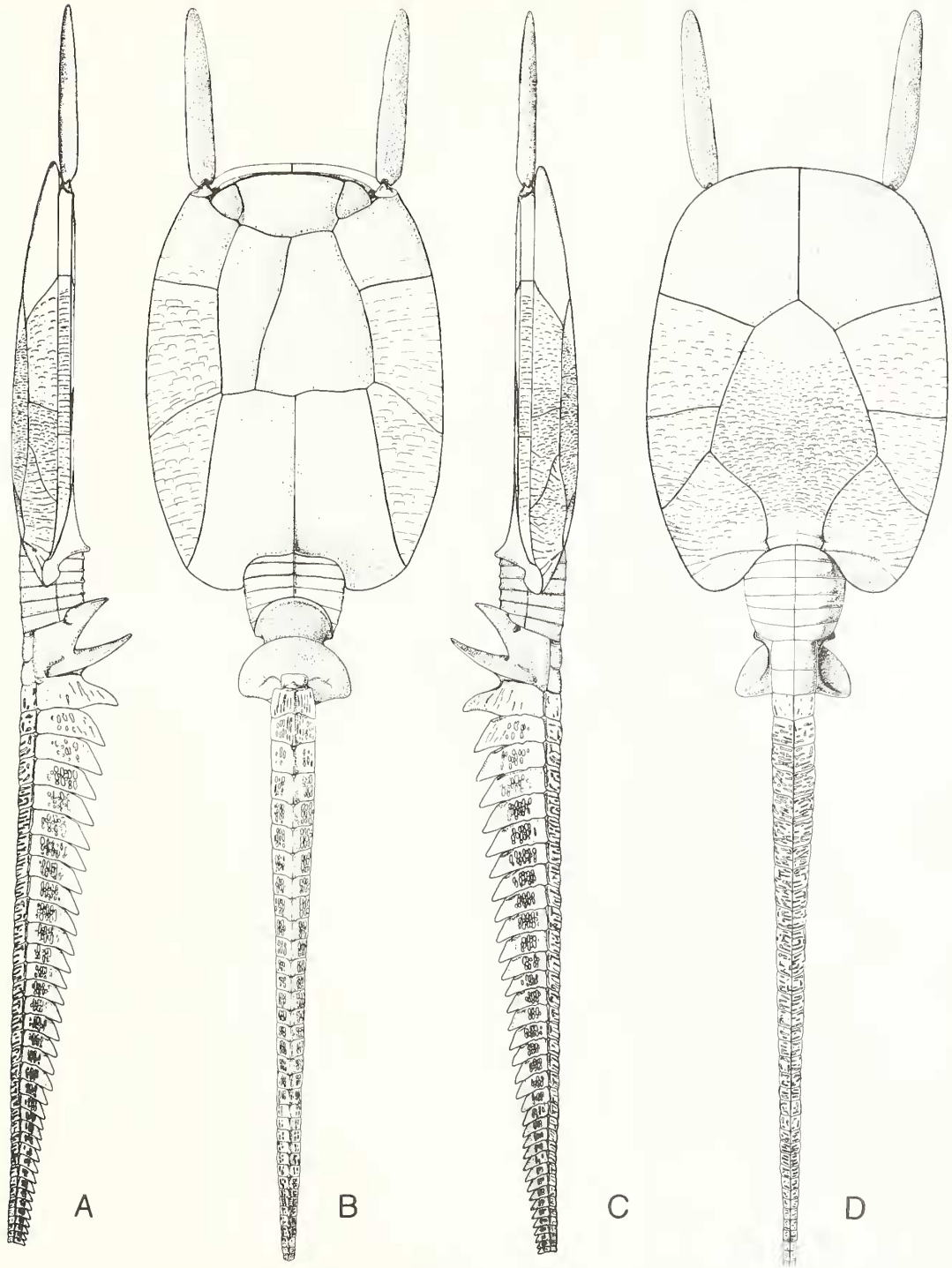
TEXT-FIG. 1. Distribution of the Ceres Subgroup, with localities of collecting sites.

		FORMATION	THICK-NESS (m)	AGE
BOKKEVELD GROUP	BIDOUW SUBGROUP	KAROOPOORT	50	
		OSBERG	55	GIVETIAN
		KLIPBOKKOP	170	
		WUPPERTAL	65	
		WABOOMBERG	200	
	CERES SUBGROUP	BOPLAAS	30	
		TRA-TRA	85	EIFELIAN
		HEX RIVER	100	
		VOORSTEHOEK	115	
		GAMKA	135	
		GYDO	160	EMSIAN

TEXT-FIG. 2. Stratigraphical column of the Bokkeveld Group.

basis of two specimens from Gamka Poort (Cape Province). For Rennie, *Placocystella capensis* and '*Placocystis*' *africanus* were likely to belong to the same genus and perhaps to the same species.

Reed's and Rennie's species were assigned to the family Placocystidae by Caster (1952), who later (1954) concluded that they were congeneric. In his revision of the Allanicytidiidae Caster and Gill, 1967, Caster (1983) mentioned *Placocystella* but did not include it in this family. Ubaghs (1967) diagnosed and figured this genus following Caster's 1954 paper. Derstler (1979) placed *Placocystella capensis* in the Mitrocystitida (*sensu* Caster 1952), presumably because oral spines are not preserved in Rennie's specimens, and kept it separate from '*Placocystis*' *africanus*, which he assigned to the Anomalocystitida (Reed's specimen shows spines). *Placocystella capensis* was reported from the two lowermost formations of the Bokkeveld Group by Oosthuizen (1984). He presumably referred to



TEXT-FIG. 3. *Placocystella africana* (Reed, 1925). Reconstruction of the external aspect. A, left lateral view; B, dorsal view; C, right lateral view; D, ventral view.

the two lowermost shaly units, the Gydo and the Voorstehoek shales, as mitrates are not known from the Gamka Sandstone. Parsley (1991) considered '*Placocystis*' *africanus* and *Placocystella capensis* as separate species and regarded them as possible members of the Allanicytidiidae, despite the incomplete knowledge of their anatomy.

The present work confirms that Reed's and Rennie's species are the same. In view of the nomenclatural problems outlined above, the denomination for the South African mitrate is *Placocystella africana* (Reed, 1925). *Placocystella capensis* Rennie, therefore, becomes a subjective junior synonym. In this paper, the reconstructions and descriptions of the mitrates and the cladistic analysis are by M. Ruta. The review of the Bokkeveld Group, the stratigraphical column and the outcrop map are by J. N. Theron.

Repositories: SM, Sedgwick Museum, Cambridge; SAM, South African Museum, Cape Town; JJS, Savill collection, Airton, Skipton, North Yorkshire; BMNH, The Natural History Museum, London. The Savill collection was kindly donated by Mr Jeremy J. Savill to the Department of Palaeontology of The Natural History Museum, London. The specimens in this collection are identified with their former catalogue numbers in parenthesis and by The Natural History Museum registration numbers.

REVIEW OF THE BOKKEVELD GROUP OF SOUTH AFRICA

Introduction. Although numerous fossils from the Bokkeveld Group were described during the first part of the last century (Thom 1830; Bain 1856; Salter 1856), it was only after 1895 that extensive research yielded a more complete picture of the distribution and stratigraphical setting of the Bokkeveld beds. Their Devonian age was confirmed by comparing their fossil faunas with those from South America and Europe (Corstorphine 1896; Clarke 1913; Reed 1925). The Bokkeveld Group forms part of the clastic Cape Supergroup, which extends for 800 km eastwards and 300 km northwards of Cape Town. The Cape Supergroup is subdivided into the basal, mainly arenitic Table Mountain Group; the middle, markedly argillaceous Bokkeveld Group; and the upper, more arenitic Witteberg Group.

Stratigraphical setting. The Bokkeveld Group consists of cyclical sequences of mainly argillaceous units alternating with arenaceous horizons. Each of these litho-units has been given formational status. The six lower formations, recognizable throughout the outcrop area, are referred to as the Ceres Subgroup (Text-fig. 1). In the west, the upper part of the sequence, designated as the Bidouw Subgroup, comprises five formations (Text-fig. 2). In the east, the laterally equivalent Traka Subgroup consists of three formations (Theron 1972; Theron and Johnson 1991). The total sequence is much thicker in the east than in the west.

Weathering of the sequence resulted in a hogsback topography: the more resistant arenitic units create ridges, whereas the softer, intervening argillaceous units weather mainly recessively and are less well exposed. The sequence represents five major, upward-coarsening, superimposed cycles, gradually replaced southwards by a relatively homogeneous mudstone-siltstone sequence. The decrease in the amount of coarse clastics is linked with a progressive thickening of the argillaceous units towards the south. The arenaceous units vary from fine-grained quartz arenites to horizontally laminated or cross-bedded immature arkosic arenites. The argillaceous units consist of dark grey

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EXPLANATION OF PLATE 1

Figs 1–4. *Placocystella africana* (Reed, 1925). Specimens in figs 1 and 2 from localities K, Klipfontein, and B, Lakenvalleidam, respectively; Ceres Subgroup, Voorstehoek Shale; specimens in figs 3 and 4 from Swaarmoed Pass, Ceres; Ceres Subgroup, Voorstehoek Shale. 1, latex cast of SAM 0135, centro-dorsal plates, upper lip and stereom structure of oral spines. 2, latex cast of SAM 0036, dorsal aspect of V6, partial head frame, dorsal fore-tail plates and anterior styloid blade. 3, latex cast of BMNH EE 5651 (JJS4), partial dorsal head skeleton and plate n. 4, latex cast of SAM 0113, anterior half of dorsal head skeleton and oral spines. All × 5.

1

2

3

4

RUTA and THERON, *Placocystella*

shale, mudstone and siltstone with thin intercalated lenses of fine- to medium-grained lithic sandstone.

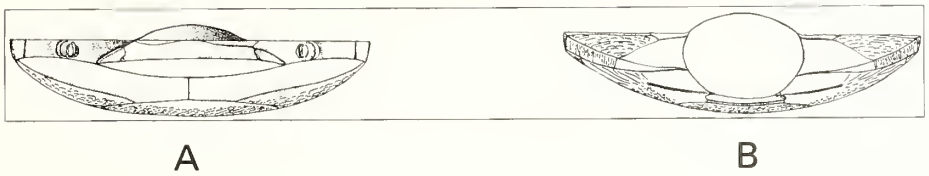
Little attention was paid in the past to the stratigraphical occurrence of the Bokkeveld fossils, and for many years no serious attempts were made to detect their zonal distributions. However, geographical differences were noted (Schwarz 1906; Theron 1972; Oosthuizen 1984). For example, brachiopods and echinoderms are commoner in the west, whereas conulariids, corals and hyoliths are prevalent in the east. Bryozoans, fish and ostracodes are rare throughout. Marine invertebrates are particularly common in the Ceres Subgroup, but occur up to the Klipbokkop Formation in the west and the Karies Formation in the east. Although present throughout the sequence, plant and trace fossils are commoner in north-western outcrops. Certain taxa occur most commonly in particular lithologies (Theron 1972; Oosthuizen 1984): trilobites and cephalopods occur mainly in argillaceous horizons; brachiopods, gastropods and bivalves can be found both in arenaceous and in argillaceous units. However, some brachiopod genera seem to have preferred sandy sediments and the infaunal bivalves are largely confined to shaly units. Crinoids are found in a wide variety of sedimentary rocks, varying from mudstone to lithic arenites. Stalk fragments are abundant, but well preserved crinoids are mainly confined to fine-grained units. This is true also for ophiuroids and blastoids, which, although rare, occur mainly in mudstone and shales or in silty shales. The overall decrease in invertebrate fossils in a northward direction, where the argillaceous units become sandier, suggests a shallowing of the basin in that direction. A decrease occurs also southwards, towards the deeper part of the basin (Theron 1970, 1972; Theron and Loock 1988).

Palaeogeographical setting. The Bokkeveld sedimentary strata record the most dynamic phase of the Cape basin development, when tectonic unrest and accelerated downwarp evolved at the Pragian-Emsian transition. The vertical stacking of the upward-coarsening sequences implies tectonically controlled regressions and transgressions (Theron 1972; Tankard and Barwis 1982). The five major cycles record the progradation of lobate, wave-dominated deltas along a coastline of moderately high marine energy (Tankard and Barwis 1982; Theron and Loock 1988). The nearshore deposits grade southwards into thick shelf mudstones. The greatest thickness is towards the eastern Cape and reflects increased downwarping in that direction.

An idealized Bokkeveld sequence consists of sediments of the shelf, delta slope and delta platform environments deposited successively during the constructional phase of delta growth and is overlain by nearshore marine reworked deltaic deposits produced during the destructional phase of delta development (Tankard and Barwis 1982). The marked change from a few thousand metres of supermature sands of the Table Mountain Group to the predominantly muddy sediments of the Bokkeveld Group throughout the Cape basin represents an overall northward advance of the shoreline and a progression of the Gydo shelf and delta slope sediments across the sand-shoal deposits of the Rietvlei Formation in the early Devonian.

The Bokkeveld mud and siltstone deposits are dark grey and preserve scattered external and internal moulds of a rich invertebrate fauna. Coquinites, where present, are relatively thin, but laterally persistent. As water depth increased, these deposits became rarer. Ebbing storm surge currents collected shells and sediment from the sea floor and carried them seawards. Eventually, hollows and storm-generated channels entrapped them in large quantities (Hiller and Theron 1988). Storm activity is also well documented in the overlying delta platform sediments, associated with the distributary mouth bar, the interdistributary bay and the tidal flat (especially in the northern facies; Theron and Thamm 1990). These sedimentary rocks consist mainly of sandstones, siltstones and mudstones. Fossil invertebrates are occasionally found in thick lenticular coquinites. Plant remains are rare. The progressive upward shallowing reflected by these environments caused impoverishment of the invertebrate fauna, as fossils are rather sparse or absent in the marine reworked sands of the delta platform. Wave and tidal activity created interspersed barrier washover sheets as well as tidal inlet and channel filling sequences.

Post-mortem transport of the organisms was generally limited. The mechanical damage to shells is minimal. Disarticulated valves occur commonly, but they rarely display signs of abrasion or



TEXT-FIG. 4. *Placocystella africana* (Reed, 1925). Reconstruction of the external aspect. A, anterior view (oral spines omitted); B, posterior view (tail omitted).

breakage. Rapid burial of individuals of various species in life position, exquisitely preserved in the Gydo and Waboomberg formations, indicates the action of gentle currents at the depositional site. A sudden influx of fine sediment, either carried by delta-feeding rivers or produced by storms generating a blanket of wave-stirred mud, may have occurred.

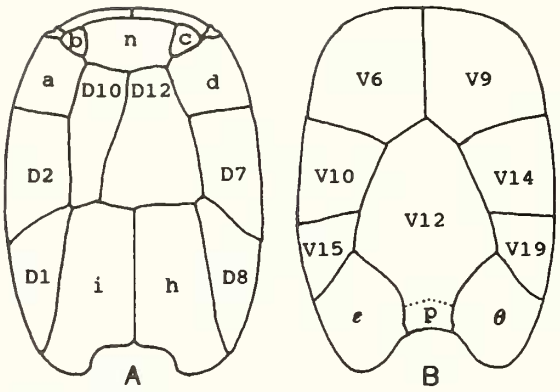
Palaeoecology. The Bokkeveld benthic community structures were discussed briefly by Boucot (1971) and Hiller and Theron (1988). A number of communities can be correlated with the depositional sub-environments of the delta complex. The tidal flat community was dominated by inarticulate brachiopods and infaunal bivalves and inhabited the sheltered, back-barrier environment. The distributary mouth bar community consisted mainly of brachiopods and occupied the relatively turbulent shallow water setting at the seaward edge of the delta platform. The delta slope community was more diverse. The brachiopods were still dominant, but infaunal bivalves, gastropods, cricoconarids and crinoids were also present. Trilobites were an important component of this community. The shelf community contained the most diverse fauna of all, with brachiopods (less than half of the total assemblage), abundant trilobites, bivalves and gastropods and a significant proportion of echinoderms, hyoliths, corals, bryozoans, conulariids and cephalopods.

In the Gydo and Gamka formations, all the above-mentioned communities are well represented. Shelf and slope communities are present in the Voorstehoek Formation. Shelf communities have also been identified in western outcrops of the Waboomberg Formation. Fossils are generally too rare for palaeoecological studies in many of the other formations. The mitrates described here occur largely in silty mudstones of the Gydo and Voorstehoek formations and belong to the shelf community. This inhabited a deep water environment, off the front of the growing delta and beyond the effects of waves and tides, which explains the deposition of fine sediment. The taxa are represented by numerous suspension feeders (brachiopods, crinoids, corals, bryozoans, epifaunal bivalves, some infaunal bivalves), a significant number of deposit feeders (some trilobites and ophiuroids, epifaunal hyoliths, most infaunal bivalves and, perhaps, mitrates), possible herbivores (some gastropods) and predators (some cephalopods).

SYSTEMATIC PALAEONTOLOGY

Superphylum DEUTEROSTOMIA Grobben, 1908
(Stem group of the Craniata?)
Family ALLANICYTIDIIDAE Caster and Gill, 1967

Diagnosis. Anomalocystitid mitrates characterized by the presence of four paired marginal ventral plates surrounding a large, centro-ventral element; plates ε and θ not sutured with each other mid-ventrally; upper lip plates highly modified to form a flexible articulation with the centro-dorsal and the antero-lateral dorsal marginal plates; styloid with transversely expanded blades.



TEXT-FIG. 5. *Placocystella africana* (Reed, 1925). A, dorsal head plate nomenclature; B, ventral head plate nomenclature.

Genus PLACOCYSTELLA Rennie, 1936

Type species. Placocystella capensis Rennie, 1936 (= *Placocystella africana* Reed, 1925).

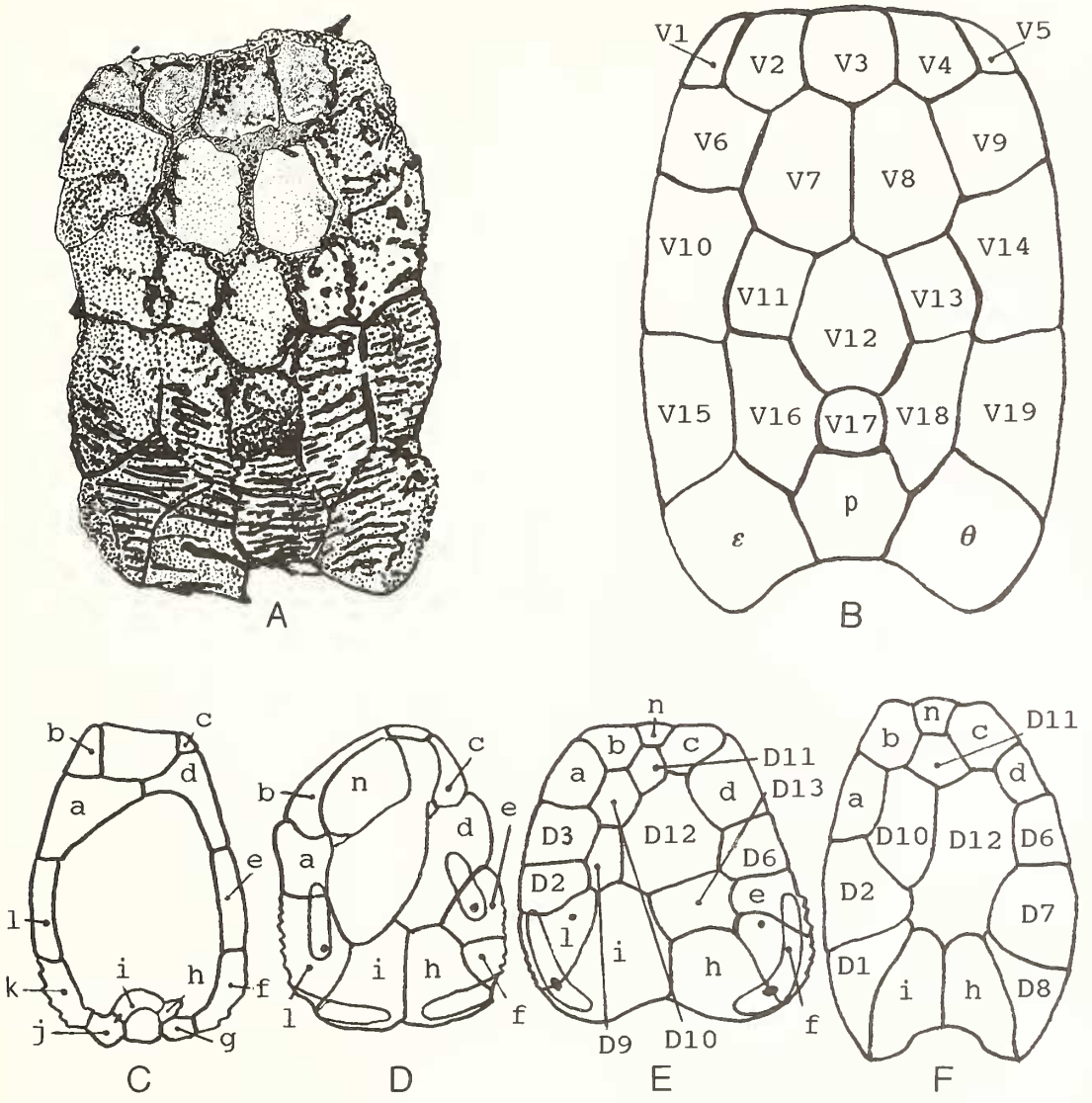
Placocystella africana (Reed, 1925)

Plates 1–8; Text-figures 3–5, 7–21

1925 *Placocystis africanus* Reed, p. 30, pl. 4, fig. 1.
1932 *Placocystites africanus* (Reed); Dehm, p. 65.
1936 *Placocystis africanus* Reed; Rennie, p. 273, pl. 31, fig. 1.
1936 *Placocystella capensis* Rennie, p. 269, pl. 31, figs 3–9.
1941 *Placocystis africanus* Reed; Chauvel, p. 217.
1941 *Placocystella capensis* Rennie; Chauvel, p. 217.
1952 *Placocystis africanus* Reed; Caster, p. 19.
1952 *Placocystella capensis* Rennie; Caster, p. 19.
1954 '*Placocystis*' *africanus* Reed; Caster, p. 145, fig. 3a–c, 4; pl. 8, figs 5–8.
1954 *Placocystella capensis* Rennie; Caster, p. 145, fig. 3d–f.
1967 *Placocystella capensis* Rennie; Ubaghs, p. 561, fig. 357, 5.
1979 '*Placocystis africanus*' Reed; Derstler, p. 102.
1979 *Placocystella capensis* Rennie; Derstler, p. 102.
1983 *Placocystella* sp. Rennie; Caster, p. 328.
1984 *Placocystella capensis* Rennie, pars; Oosthuizen, p. 139.
1989 *Placocystella* sp. Rennie; Craske and Jefferies, p. 95.
1990 *Placocystella capensis* Rennie; Cripps, p. 59.
1991 *Placocystis africanus* Reed; Parsley, p. 16.
1991 *Placocystella capensis* Rennie; Parsley, p. 16.
1994 *Placocystella capensis* Rennie; Cripps and Daley, p. 125.

Holotype, type locality and type horizon. SM A.3044; Buffelskraal, Hex River Pass, Gydo Shale; 33°24′S, 19°48′E (Text-fig. 7A).

Diagnosis. Plate D10 as long and half as wide as D12; anterior margin of plates V6 and V9 asymmetrical and visible in dorsal view; oral spines robust and cigar-like; riblets on plates D1, D2, D7, D8, V10, V12, V14, V15, V19, p, ε and θ; lateral ribs on ε, θ, V15 and V19; transverse keels on ε and θ; anterior, fan-like styloid blade with radial thickenings; posterior styloid blade parabolic in outline and smooth; first hind-tail ossicle more robust than successive ossicles and with fine striations; successive ossicles with knobs; hind-tail plates with irregular, mainly transverse ridges and a dorsal, horizontal keel.



TEXT-FIG. 6. A–B, *Bokkeveldia oosthuizeni* gen. et sp. nov.; A, drawing of the holotype; B, nomenclature of the ventral head plates. C–F, nomenclature of the dorsal head plates in cornutes and mitrates; C, the cornute *Reticulocarpos hanusi*; D, the mitrate *Chinianocarpos thorali*; E, the mitrate *Mitrocystites mitra*; F, the mitrate *Mitrocystella incipiens* (C–F redrawn and simplified after Jefferies 1986).

Material, localities and horizons. SAM 0002–0003, 0060–0061, 0102–0104; locality D, Gydopas, Gydo Shale; 33°13′55″S, 19°19′35″E. SAM 0072; locality L, Doornkloof, Gydo Shale; 33°23′20″S, 21°08′45″E. SAM 0009, 0011–0015, 0085–0086, 0106–0110, 0112–0114; locality A, Klipfontein, Voorstehoek Shale; 33°21′20″S, 19°30′45″E. SAM 0049–0051, 0092, 0094–0095, 0101, 0132, 0135; locality K, Klipfontein, Voorstehoek Shale; 33°21′25″S, 19°30′25″E. SAM 0035–0036; locality B, Lakenvalleidam, Voorstehoek Shale; 33°19′55″S, 19°33′15″E. SAM 0139; locality J, Lakenvalleidam, Voorstehoek Shale; 33°19′55″S, 19°33′15″E. BMNH EE 5648–5649 (JJS1–2), BMNH EE 5651 (JJS4), BMNH EE 5653–5654 (JJS6–JJS7), BMNH EE 5656 (JJS9), BMNH EE 5658 (JJS11), BMNH EE 5660 (JJS13), BMNH EE 5662–5667 (JJS15–20); Swaarmoed Pass,

Ceres, Voorstehoek Shale; 33°21′20″S, 19°30′40″E. BMNH EE 5657 (JJS10); Sewenweekspoort, Voorstehoek Shale; 33°21′50″S, 21°22′E. BMNH EE 5668 (JJS21); Tunnel Siding, Voorstehoek Shale; 33°25′S, 19°46′E. BMNH E23684–23685 (plaster replicas of SAM 9701 and SAM 9700 respectively; Gamka Poort, Gydo Shale; 33°18′S, 21°38′E). Most of the South African Museum specimens were collected by Dr R. P. S. Jefferies, Mr J. J. Savill and Dr J. N. Theron in January 1993.

Methods of study and plate terminology. The fossils were cleaned in ethanolamine thioglycollate. The reconstructions are based mainly on camera lucida drawings of latex casts coated with ammonium chloride to accentuate relief.

In most mitrocystitids and anomalocystitids, the dorsal head skeleton is morphologically conservative, but the ventral head plates vary in number, arrangement, shape and position. Here, the same notation is given to putatively homologous plates in different species. In the case of *Placocystella africana*, D followed by a numeral applies to the centro-dorsal and to those marginal plates believed to correspond with like-named plates in *Mitrocystites mitra* and *Mitrocystella incipiens* (D1, D2, D7, D8, D10 and D12; Text-fig. 6E–F), whereas the lower-case h, i, a, b, c and d apply to those marginal plates which are perhaps homologous with their namesakes in *Reticulocarpos hanusi* (Text-fig. 6C; discussion in Jefferies and Prokop 1972). Most of the ventral head plates are labelled as V followed by a numeral, a new system based on the ventral skeleton of *Bokkeveldia oosthuizeni* gen. et sp. nov. (V6, V9, V10, V12, V14, V15 and V19; Text-fig. 6A–B). Exceptions are plates p, homologous with their namesake in *Barrandeocarpus norvegicus* (Craske and Jefferies, 1989), and ε and θ, possibly homologous with like-named elements in *Prokopicystis mergli* (Cripps, 1989).

DESCRIPTION

External anatomy of the head

Dorsal skeleton (Text-figs 3B, 5A, 7B–C, 8–9, 10A; Pl. 1, figs 1–4; Pl. 2, figs 2–4; Pl. 4, figs 2–3, 6; Pl. 6, figs 5–6). The head, elliptical in plan view and bilaterally symmetrical, is mostly flat dorsally. The dorsal skeleton consists of two centro-dorsal and 11 marginal plates (Text-fig. 5A). The postero-median half of D1 and D8 and the posterior third of i and h slope gently downward and laterally. All marginals except n form pairs of plates along the lateral margins of the head. Each member of a pair is almost a mirror image of the opposite plate.

Plates i and h form most of the postero-dorsal skeleton and meet along a straight, mid-dorsal suture. Their postero-median margins form a ridge, underneath which is the dorsal half of the posterior head excavation (Text-figs 8, 9A; Pl. 1, figs 2–3; Pl. 2, figs 2–3; Pl. 4, figs 3, 6; Pl. 6, figs 5–6). The lateral margins of i and h are gently sinuous. The anterior margin of i is divided into a left shorter and a right longer segment sutured with D10 and D12 respectively. The anterior margin of h contacts D12 and is concave rearward medially and straight laterally (Text-figs 3B, 5A, 9A, 10A; Pl. 1, figs 1–4; Pl. 2, fig. 3; Pl. 4, fig. 2; Pl. 6, fig. 5). The postero-lateral margins of i and h are rounded and contribute to the postero-lateral angles of the head. The outer margins of plates i, D1, D2 and a on the left, and of plates h, D8, D7 and d on the right are projected downward and form the lateral head walls. The anterior part of the dorsal skeleton forms a right angle with the lateral walls. At the level of D1 and D8 this angle becomes acute. This slope change begins about half-way along the lateral walls.

D1 and D8 are triangular elements. The anterior margin of D1 is concave rearward and medianward. The anterior margin of D8 is concave rearward and medianward anteriorly, and forward and rightward posteriorly

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EXPLANATION OF PLATE 2

Figs 1–4. *Placocystella africana* (Reed, 1925). Specimens in figs 1, 3–4 from locality A, Klipfontein; Ceres Subgroup, Voorstehoek Shale; specimen in fig. 2 from locality D, Gydopas; Ceres Subgroup, Gydo Shale. 1, latex cast of SAM 0106, partial ventral steinkern, partial ventral surface of dorsal head skeleton, external aspect of some ventral head plates and position of the anterior boundary of the posterior coelom. 2, latex cast of SAM 0060, rearmost part of the dorsal head skeleton. 3, latex cast of SAM 0110, oral spines and partial dorsal head skeleton; a button-like lump is visible on the partially exposed dorsal surface of V15. 4, latex cast of SAM 0108, partial of the dorsal head skeleton, left oral spine and part of the lower lip. All × 5.

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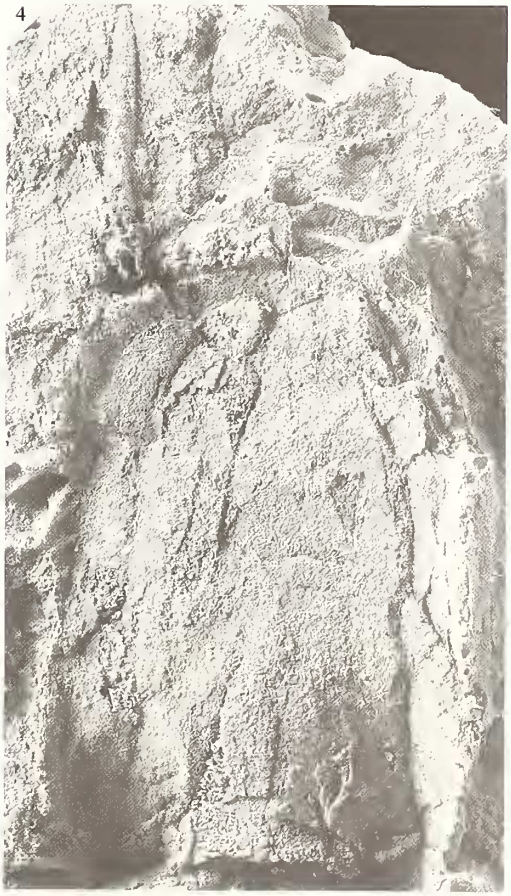
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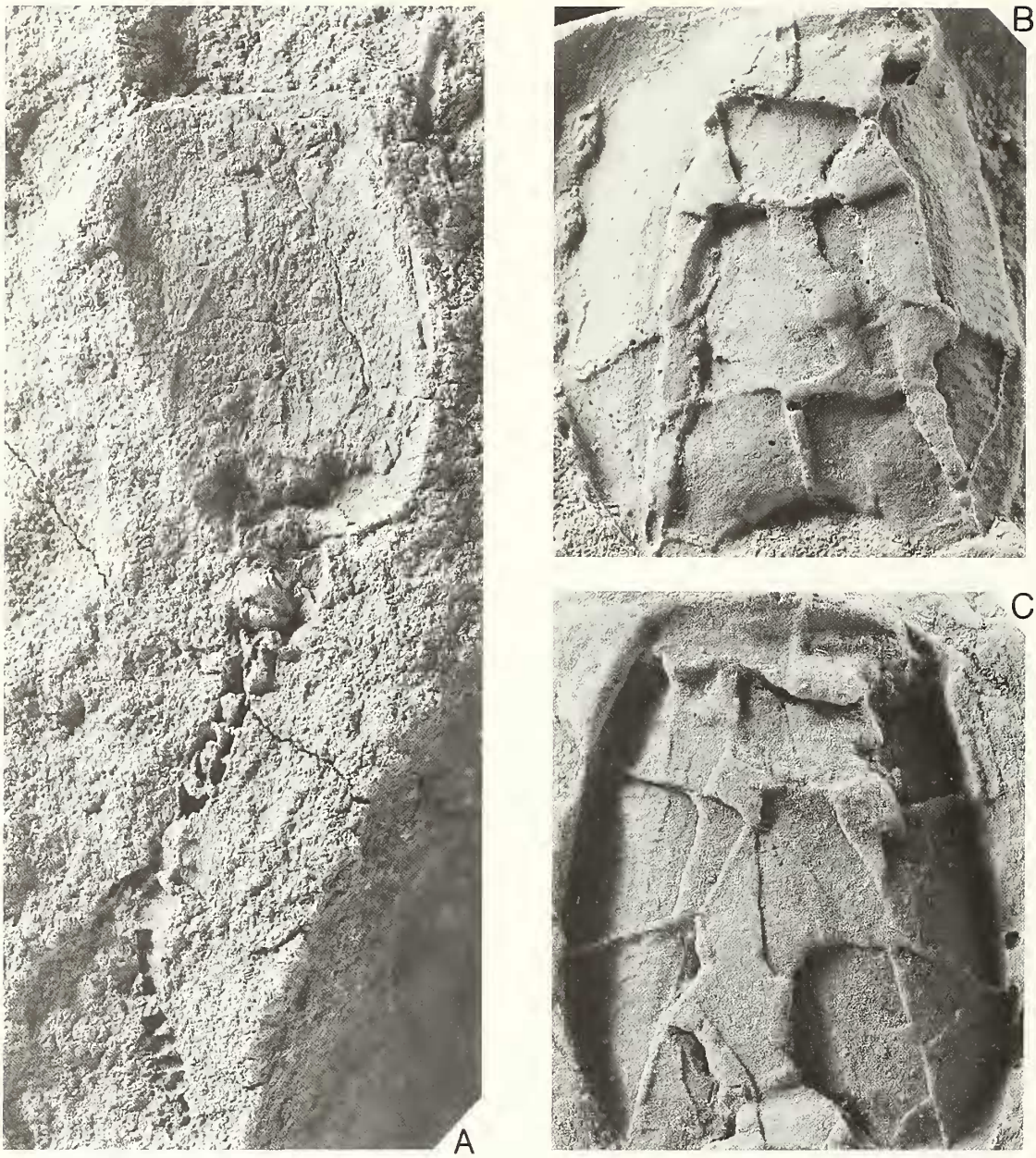
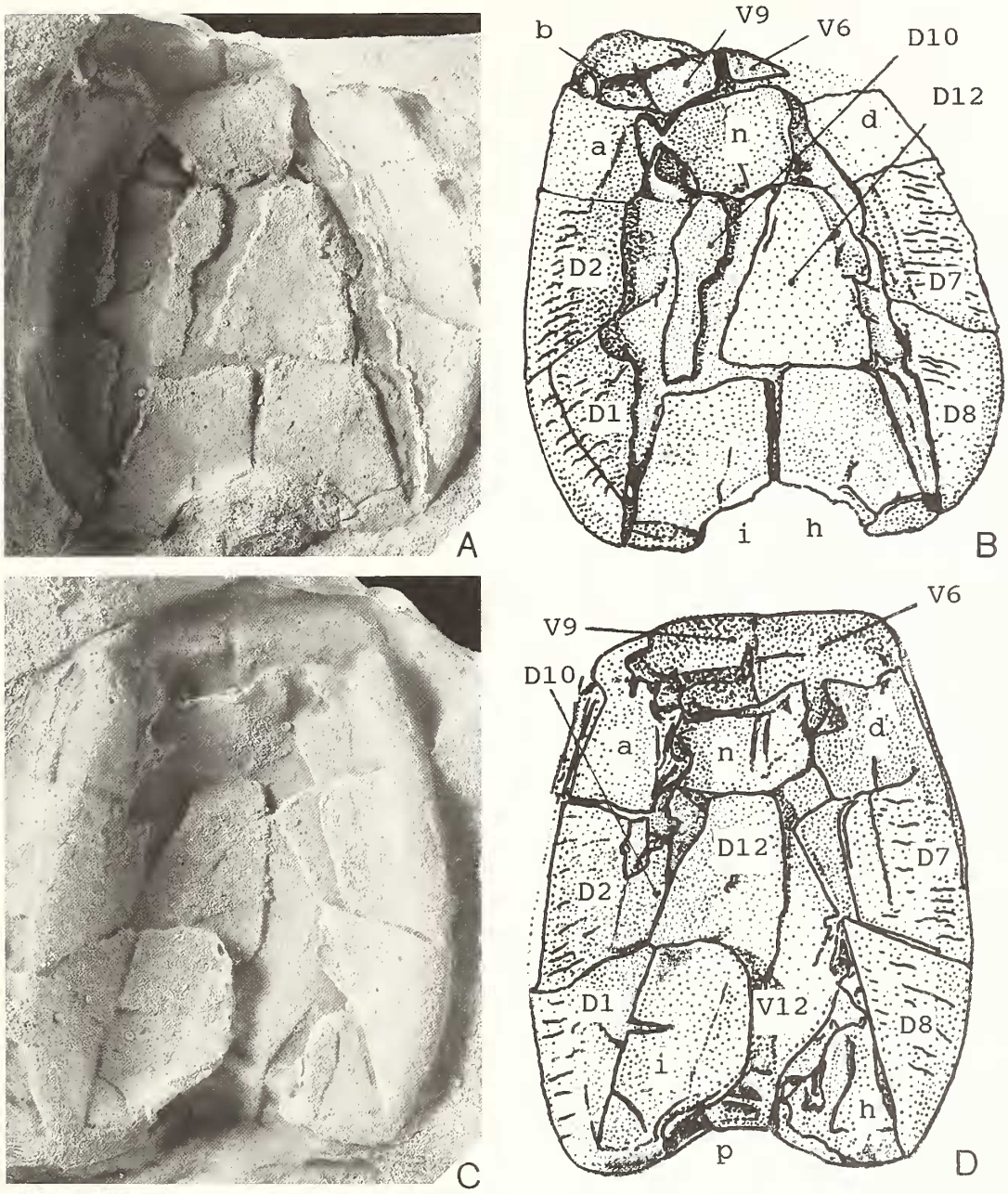
RUTA and THERON, *Placocystella*



TEXT-FIG. 7. *Placocystella africana* (Reed, 1925). A, holotype, SM A.3044; Buffelskraal, Hex River Pass; Ceres Subgroup, Voorstehoek Shale; natural external mould of ventral head skeleton and partial natural internal mould of mid- and hind-tail; × 5. B, BMNH E23684, plaster replica of SAM 9701; northern entrance of Gamka Poort; Ceres Subgroup, Gydo Shale; external mould of dorsal head skeleton; × 4. C, BMNH E23685, plaster replica of SAM 9700; horizon and locality as B; external mould of dorsal head skeleton and partial ventral internal mould; × 4.



TEXT-FIG. 8. *Placocystella africana* (Reed, 1925). A, latex cast of BMNH E23684; ×4. B, interpretative sketch. C, latex cast of BMNH E23685; ×4. D, interpretative sketch.

(Text-figs 3B, 9A, 10A; Pl. 1, fig. 1; Pl. 6, figs 5–6). D2 and D7 are trapezoidal. The median margin of D7 follows the curvature of the right head margin. The straight, median margin of D2 is not parallel to the body axis (Text-fig. 9; Pl. 1, figs 2–4).

The sub-quadrangular plates a and d carry the articulation of the oral spines antero-laterally. The median part of the anterior margin of a forms a short junction with n (Pl. 1, figs 1, 4; Pl. 4, fig. 6), whereas its lateral part contacts b. The junction between n and d (Text-figs 9A, 10A; Pl. 1, figs 3–4) corresponds to the median part of the anterior margin of d (Pl. 5, fig. 6). The lateral part of this margin contacts c.

Plates b, n and c form the upper lip. Plate b is wedge-shaped and its longitudinal axis faces forward and leftward. Plate c seems to be shorter than b and is more equilateral. Its longitudinal axis faces forward and rightward (Text-figs 9A, 10A, 11; Pl. 1, fig. 1; Pl. 2, fig. 3). Plate n forms most of the upper lip and has a slightly convex dorsal surface. Its left margin contacts b and a, whereas its right margin contacts c and d. Its anterior margin is convex outward. Its posterior margin is divided into two unequal segments forming a triple junction with D10 and D12: the left segment is sinuous, whereas the right segment is straight (Text-fig. 9A; Pl. 1, figs 1, 3–4). The junctions of b, n and c with a, D10, D12 and d are cylindrically rounded (Text-fig. 9A; Pl. 1, figs 1, 3) and perhaps allowed the upper lip to be lifted in life.

D10 is five- or six-sided; D12 is seven-sided. The D10/D12 suture, divided into a sinuous anterior and a straight posterior part, runs from the mid-point of the posterior margin of n to the anterior margin of i.

Ventral skeleton (Text-figs 3D, 5B, 10B; Pl. 2, fig. 1; Pl. 3, figs 1–4; Pl. 4, figs 4–5; Pl. 5, figs 2–5; Pl. 8, fig. 2). The ventral skeleton is a rigid, gently convex structure of ten plates, nine of which are marginals (Text-fig. 5B). All ventral marginals except p form pairs. Each member of a pair is almost a mirror image of the other.

V12, sometimes found articulated only with plates ε, θ and p, is diamond-shaped and almost bilaterally symmetrical (Text-fig. 10B; Pl. 3, figs 2–4; Pl. 5, figs 3–5; Pl. 8, fig. 2) and contacts the ventral marginals along its nine sides. In adults of *P. africana*, the posterior margin of V12 is fused with p (Pl. 5, figs 4–5), but one small, presumably young individual seems to show a distinct p/V12 suture (Pl. 5, fig. 3).

Plates ε and θ form the postero-ventral skeleton and part of the posterior head surface. In lateral view, their ventral curvature is more prominent than that of other ventral plates. Plates ε and θ contact: h and i posteriorly; the postero-lateral sides of V12 and the lateral margins of p medially; and V15 and V19 anteriorly along two sinuous sutures.

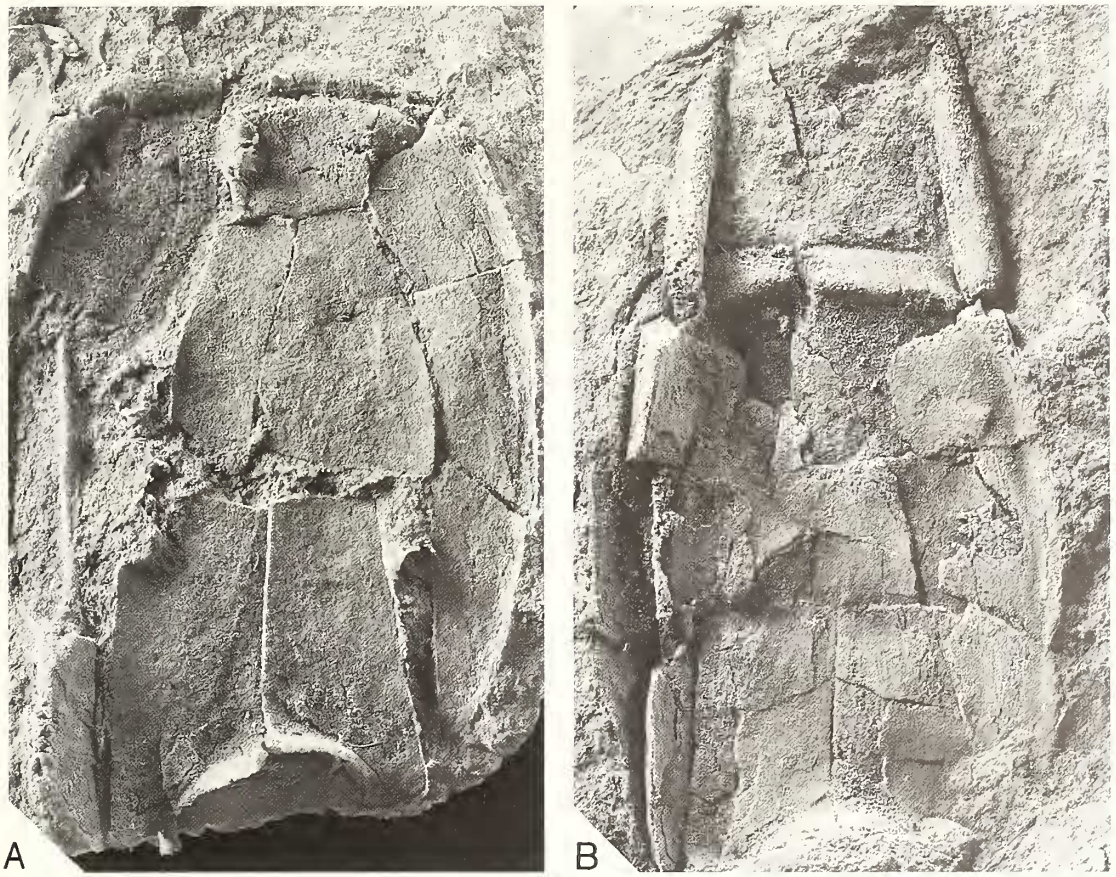
V15 and V19, the smallest ventral marginals, are trapezoidal. V10 and V14 are slightly larger than V15 and V19, but are smaller than V6 and V9. V6 and V9 occupy the anterior third of the head floor and contact each other along a straight, mid-ventral suture. Postero-medially, they are sutured with the anterior sides of V12. These are not symmetrical, as the right side is slightly longer than the left. The anterior margins of V6 and V9, visible in dorsal view, show a gentle anterior surface, a rounded upper edge and a steep posterior surface (Text-figs 8–9, 11; Pl. 1, figs 2, 4; Pl. 4, fig. 3; Pl. 5, fig. 6).

Ornament (Text-figs 3–4, 7B–C, 8, 10; Pl. 3, figs 1–4; Pl. 5, figs 2–5; Pl. 8, fig. 2). This consists of ribs, riblets and broken ribs. The ribs are transversely elongate with an anterior steeper and a posterior gentler slope (cuesta-like profile). The distance between each rib is about the same in individuals of different sizes, which are presumed to be of different ages, suggesting that new ribs were formed as the head grew. The riblets are sub-rectangular to crescentic sculptures, densely grouped and particularly numerous on V12. Like ribs, they are cuesta-like. Their anterior margin shows minute denticles. The broken ribs are irregular lines marking the spatial transition from ribs to riblets and are sometimes visible on the middle and posterior parts of the lateral head walls (Text-fig. 10; Pl. 3, fig. 2).

Widely spaced riblets on D1, D2, D7 and D8 (Text-fig. 10A) sometimes become confluent and give rise to irregular, sinuous ribs. Along the median margins of D1, D2, D7 and D8 and behind the anterior margins of D2 and D7 the ornament is absent. D10, D12, a, b, n, c, d, h and i are usually smooth, but some specimens show riblets on a and d (Text-fig. 8).

V6, V9 and the anteriormost part of V12 are smooth. V10 and V14 have few widely spaced riblets stopping behind their anterior margins. The anterior half of both V15 and V19 carries widely spaced riblets, whereas the postero-lateral half shows ribs. These become broken and sinuous medially and continue on the anteriormost surfaces of ε and θ. V12 has closely spaced riblets confined to its posterior two-thirds (Text-fig. 10B; Pl. 3, figs 1–4; Pl. 5, figs 3–5).

Two robust keels run from the postero-lateral angles of p to the centre of the posterior third of ε and θ (Pl. 5, figs 3–5). The external surface of these two plates in front of and behind the keels is smooth and elliptical in outline and continues medially on plate p. Riblets cover a narrow transverse area just behind the anterior margin of p. The lateral surfaces of ε and θ bear ribs which become wavy and irregular anteriorly. Near the anterior half of the median margins of these two plates the ornament consists mainly of riblets.



TEXT-FIG. 9. *Placocystella africana* (Reed, 1925). A, latex cast of BMNH EE 5649 (JJS2); Swaarmoed Pass; Ceres Subgroup, Voorstehoek Shale; almost complete dorsal head skeleton and antero-lateral part of dorsal surface of V9; × 5. B, latex cast of SAM 0106; locality A, Klipfontein; Ceres Subgroup, Voorstehoek Shale; partial dorsal head skeleton, anterior margin of ventral head skeleton and oral spines; × 5.

Oral spines (Text-figs 3, 5, 7A, 9B, 11; Pl. 1, figs 1, 4; Pl. 2, figs 3–4; Pl. 3, figs 3–4; Pl. 4, figs 1, 3–6; Pl. 5, fig. 6; Pl. 6, figs 5–6; Pl. 8, fig. 2). The spines, elliptical in cross section throughout their length, taper distally. The proximal dorsal surface of each spine slopes gently rearward and downward towards a dorso-ventrally elongate socket. Two facets are present at the base of each spine. One of these facets is lateral and twice as wide as the other, which is median to the socket (Text-fig. 11; Pl. 3, fig. 4; Pl. 5, fig. 6; Pl. 6, fig. 6). The spines are articulated to the thickened antero-lateral angles of a and d (Text-figs 3B, 4A, 9, 11; Pl. 4, fig. 3; Pl. 5, fig. 6; Pl. 6, fig. 6). The attachment areas comprise a flat, sub-circular areola with a stout process which occupies a median position on it. The process carries a low platform, on top of which is a smooth, dorso-ventrally elongate tubercle which fits into the spine socket. The spines probably swept mainly horizontally in life, but the plane of sweep could probably be adjusted vertically to some extent.

Tail

As in all mitrates, the tail of *P. africana* consists of three parts: fore-, mid- and hind-tail, in order of increasing distance from the head.

Fore-tail (Text-figs 3, 10A; Pl. 1, fig. 2; Pl. 4, fig 3; Pl. 6, figs 1–5; Pl. 8, fig. 4). The fore-tail skeleton consists of calcitic rings (the highest recorded number is six) enclosing a lumen, presumably occupied in life by muscle. Each ring is made of four rigidly sutured plates: left and right dorsal, and left and right ventral. The ventral and dorsal plates of one side meet along a flat, horizontal suture.

Each ventral plate consists of two parts, gently convex outward and smooth-surfaced. The smaller, lower part forms most of the ventral aspect of the fore-tail, whereas the larger, upper part contributes to most of its lateral surface (Pl. 6, fig. 1).

Like the ventral plates, each dorsal plate shows two parts. The lower is gently convex outward and contributes to the lateral surface of the fore-tail. The upper is slightly concave outward. The median part of the upper surface of each dorsal plate is upturned and forms a mid-dorsal keel with its antimere. The dorsal plates have a rounded, postero-median angle and a low posterior ridge (Pl. 6, fig. 3). The fore-tail was flexible in life, as suggested by the fact that each ring overlaps its posterior successor (Pl. 1, fig. 2) and by modalities of preservation (Pl. 8, fig. 2).

Mid-tail (Text-figs 3, 10A, 17; Pl. 1, fig. 2; Pl. 4, fig. 3; Pl. 5, fig. 1; Pl. 6, figs 1, 5–6; Pl. 7, fig. 9; Pl. 8, figs 1, 4, 9). The mid-tail skeleton consists of a dorsal element, the styloid, and paired ventral plates. The number of ventral plates is uncertain. Two lumps visible below the right ventral margin of the styloid of a specimen (Pl. 7, fig. 9) are perhaps remnants of two right plates. The anterior region of the styloid decreases anteriorly in height (Pl. 7, fig. 9) and sends out a process (ap; Text-fig. 17) which fits into the distal part of the fore-tail lumen (Pl. 4, fig. 3; Pl. 6, fig. 5; Pl. 8, fig. 4). This process shows a deep antero-ventral excavation (he; Text-fig. 17; Pl. 5, fig. 1; Pl. 8, fig. 9), presumably for muscle insertion.

The styloid bears two transverse blades (asb and psb; Text-fig. 17). The smaller anterior blade is nearly semicircular in outline viewed from the exterior. Its anterior face is flat and slightly inclined anteriorly and downward and bears five or six radial thickenings (rt; Text-fig. 17) near its outer margin. A depression (od; Text-fig. 17; Pl. 5, fig. 1) is present between each thickening. The smooth posterior surface of the blade has a concave profile in lateral view and is transversely convex (Pl. 7, fig. 9). It slopes downward and rearward, merges into the dorsal styloid surface and continues ventro-laterally. The free margin of the anterior blade is blunt. Its thick ventro-lateral ends turn inward and slightly downward, merging into the lateral styloid surfaces.

The posterior blade is about twice as tall and wide as the anterior blade, has a parabolic outline in anterior view and is set lower than the anterior blade. Its anterior and posterior surfaces are mostly parallel to each other but diverge ventrally, so that the blade thickens in its lower third. The anterior surface is slightly concave in lateral view and joins the dorsal styloid surface vertically. The posterior surface is convex in lateral view and slightly depressed in its lower half. The dorsal part of the free margin of the posterior blade is sharp. Its ventro-lateral angles are thicker than the free margin and join the lateral styloid surfaces at a right angle (Text-fig. 17; Pl. 8, fig. 9). The antero-ventral styloid excavation (Pl. 5, fig. 1; Pl. 8, figs 1, 9) is smooth and roughly semicircular in anterior view. Its central area is occupied by a semi-oval pit (sp; Text-fig. 17), posterior to which is a longitudinal groove (flg; Text-fig. 17).

The groove and the pit can be compared with similar structures in other mitrates. In *Eumitrocystella savilli* (Beisswenger 1994, figs 3g, 8a–b), two 'horns' project upward into the styloid cusps both from the anterior excavation and from the posterior interossicular cavity and represent the infilling of deep pits in the skeleton. Analogous 'horns' are carried by the posterior interossicular cavities of the first few hind-tail ossicles. These structures were interpreted as resorption canals by Beisswenger, although, in fact, there is no obvious reason for thinking that they resulted from resorption. Similar horn-shaped canals project from the posterior interossicular cavities of the tail ossicles in *Ateleocystites guttenbergensis* (Kolata and Jollie, 1982). A pit in the

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EXPLANATION OF PLATE 3

Figs 1–4. *Placocystella africana* (Reed, 1925). Specimens in figs 1–3 from Swaarmoed Pass, Ceres; Ceres Subgroup, Voorstehoek Shale; specimen in fig. 4 from locality A, Klipfontein; Ceres Subgroup, Voorstehoek Shale. 1, latex cast of BMNH EE 5656 (JJS9), plate θ. 2, latex cast of BMNH EE 5648 (JJS1), almost complete external aspect of ventral head skeleton with the distribution of riblets and ribs and partial ventral surface of h, D7 and D8; dorsal cup of right pyriform body partially preserved. 3, latex cast of BMNH EE 5651 (JJS4), ventral ornament, ventral fore-tail plates and right oral spine. 4, latex cast of SAM 0011, ventral head skeleton and articulation facets of the oral spines. All $\times 5$.

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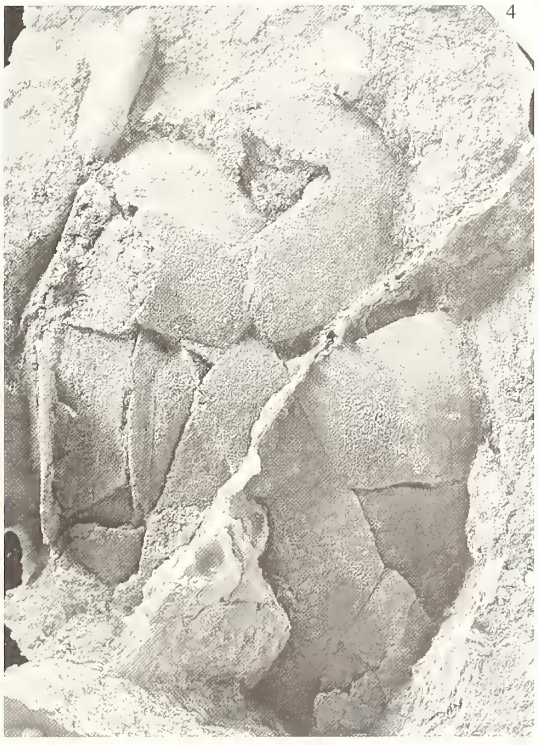

4

RUTA and THERON, *Placocystella*

antero-ventral excavation of the styloid of *Mitrocystites mitra* and *Mitrocystella incipiens* (Jefferies, pers. comm.) is in the same position as the semi-oval pit of *P. africana*.

Behind the antero-ventral excavation, the ventral styloid surface is vaulted and delimited laterally by two stout, vertical processes (vlp; Text-fig. 17). Each process has a lateral face, merging into the lateral walls of the styloid, and a median face, which joins the vaulted ventral styloid surface. The lateral and median faces of each process meet along a blunt ventral keel (vk; Text-fig. 17). The left and right keels diverge outward posteriorly. The posterior surfaces of the processes are badly preserved. Their anterior surfaces bear a small, oval shallow area (osa; Text-fig. 17). The processes contacted the mid-tail plates in life, but the nature of this contact cannot be reconstructed.

The ventral styloid surface is shown in Text-figure 17; it carries a poorly preserved longitudinal groove which probably housed the notochord/nerve chord complex in life. A pair of pits is visible on both sides of this groove. Each pit sends out a median sulcus perpendicular to the groove. The pits and the sulci are considered as traces of spinal ganglia and spinal nerves respectively (Jefferies 1986).

Hind-tail (Text-figs 3, 7A, 18–19; Pl. 7, fig. 9; Pl. 8, figs 2–3, 5–9). Articulated tails are rare, but isolated ossicles are common. The highest recorded number of hind-tail segments is 35. Each segment consists of a dorsal ossicle and two ventral plates. The plates (Pl. 7, fig. 9) are rectangular in lateral view and convex outward. The ventral hind-tail surface is rounded in cross section. The two plates of a segment meet mid-ventrally along a flat suture, ensuring a certain degree of rigidity. This rigidity is also suggested by the fact that ossicles and plates show a coarse ornament, presumably for a gripping action in life (see Jefferies 1984). The plates bear thick, transverse ridges, the shape and number of which vary in different plates, and a keel below their dorsal margins. The anterior and posterior plate margins are sinuous. The antero-dorsal angle of each plate contacts the postero-ventral angle of the preceding ossicle.

The most anterior ossicle is slightly larger than the others and its posterior margin is recurved in lateral view (Pl. 7, fig. 9). It also shows faint striations dorso-laterally. The second ossicle shows both striations and small knobs. All more posterior ossicles have knobs on their lateral surfaces, but no striations. The knobs (kn; Text-fig. 19A) vary in number, size and distribution in different ossicles and, like the ventral plate ridges, they presumably gripped sediment in life.

The ossicles are triangular in cross section. Their lateral faces are gently convex outward and meet along a mid-dorsal edge (mde; Text-figs 18A, 19A) which slopes forward and downward. Its posterior end is the dorsal apex (da; Text-figs 18, 19A).

Each ossicle (Pl. 8, fig. 5) has an anterior, a posterior, a ventral and two lateral surfaces. The dorsal half of the anterior surface is occupied by an oval depression (aod; Text-fig. 18A), delimited ventro-laterally by two ascending ridges (ar; Text-fig. 18A). These ridges approach the median plane of the ossicle ventrally, but do not contact each other. They diverge dorso-laterally and become confluent with the central part of the thick anterior ossicular margins (aom; Text-fig. 18A). The oval depression is delimited dorso-laterally by the dorsalmost parts of the two anterior ossicular margins, merging into the anterior end of the mid-dorsal edge. The dorsal third of the oval depression is much deeper than the ventral two-thirds and is cone-shaped (ce; Text-fig. 18A). The deepest part of it is occupied by a small circular pit. The ventral two-thirds of the oval depression

EXPLANATION OF PLATE 4

Figs 1–6. *Placocystella africana* (Reed, 1925). Specimen in fig. 1 from locality D, Gydopas; Ceres Subgroup, Gydo Shale; specimens in figs 2–4 from Swaarmoed Pass, Ceres; Ceres Subgroup, Voorstehoek Shale; specimen in fig. 5 from locality A, Klipfontein; Ceres Subgroup, Voorstehoek Shale; specimen in fig. 6 from Tunnel Siding, De Doorns; Ceres Subgroup, Voorstehoek Shale. 1, latex cast of SAM 0061, isolated oral spine and V9. 2, latex cast of BMNH EE 5662 (JJS15), central part of the postero-dorsal head skeleton; note the different shapes of the anterior margins of h and i. 3–4, latex casts of part and counterpart of SAM 0114: 3, partial dorsal aspect of the head, anterior margin of lower lip, spine articulations, fore-tail rings surrounding the styloid and anterior styloid blade; 4, partial ventral aspect of the head; note the impression left by the partial course of the oblique ridge; right oral spine visible in ventral view. 5, latex cast of SAM 0106, partial anterior area of ventral head steinkern and stereom structure of the oral spines. 6, latex cast of BMNH EE 5668 (JJS21); note the articulation of the upper lip plates and the optic foramen delimited by the hypocerebral processes. All × 5.

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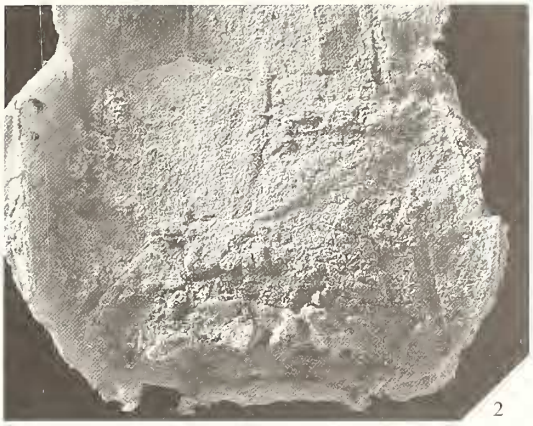
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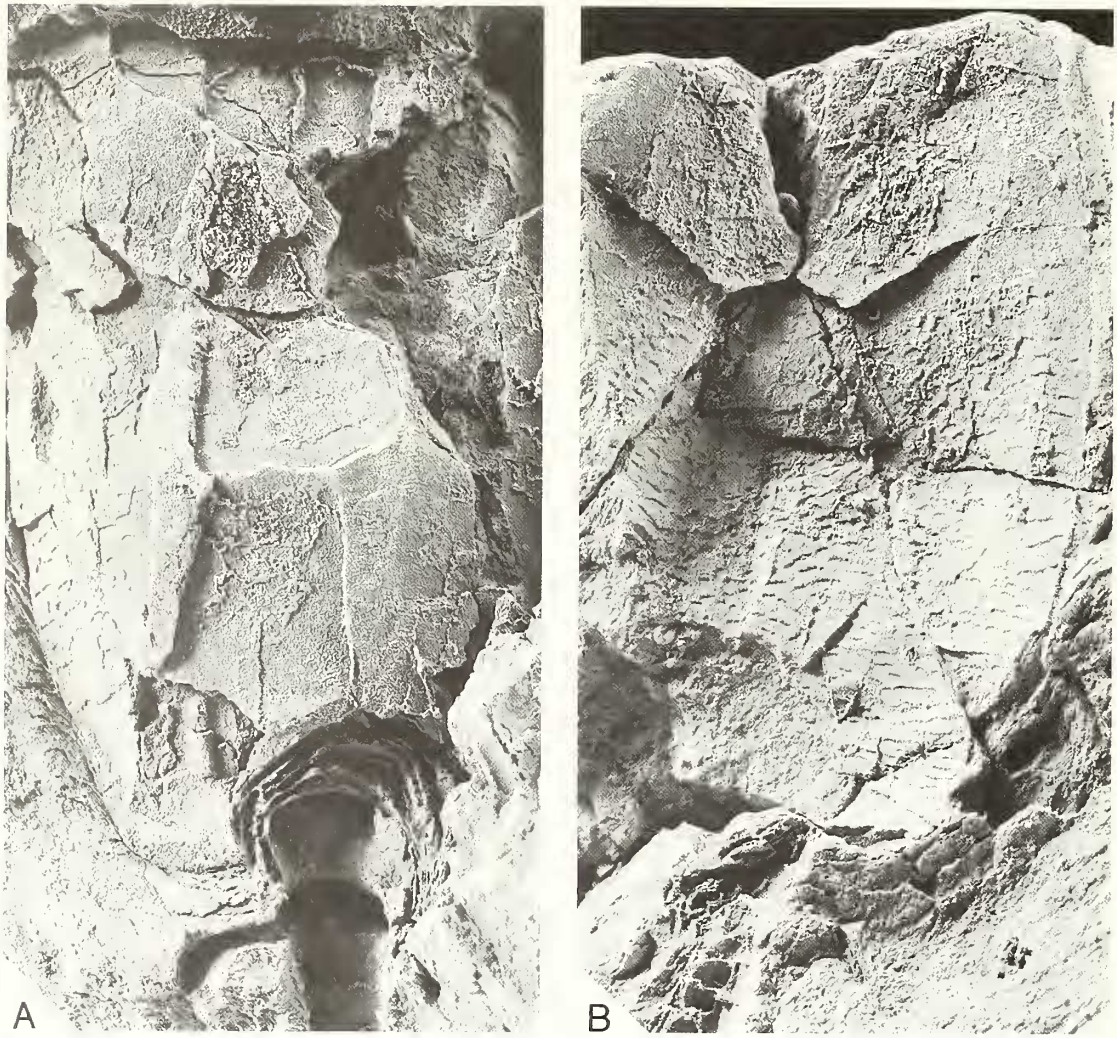
RUTA and THERON, *Placocystella*



TEXT-FIG. 10. *Placocystella africana* (Reed, 1925). A–B, natural external mould of dorsal and ventral head skeleton of SAM 0104; locality D, Gydopas; Ceres Subgroup, Gydo Shale; distribution of ribs and riblets; both × 5.

houses a shallow, anterior interossicular groove (aig; Text-fig. 18A), flanked on both sides by a thin, vertical ridge (vr; Text-fig. 18A). The latter becomes fainter dorsally and ventrally before disappearing.

The ventral half of the anterior ossicular surface bears two shallow triangular facets (tf; Text-fig. 18A), delimited dorso-laterally by the anterior ossicular margins, dorso-medially by the ascending ridges and ventrally by the upper surface of two articulation bosses (see below). Each facet sends out a ventro-lateral groove which joins a semi-elliptical depression (sd; Text-figs 18A, 19B). Each articulation boss (ab; Text-figs 18A, 19B) is shaped like an inverted 'L', the vertical arm of which is concave laterally and forms a continuous surface with the above-mentioned semi-elliptical depression. The median surface of the lower arm contributes to the mid-ventral groove (see below). The horizontal arm of each boss shows: a flat upper face joining the triangular facet posteriorly; a sausage-shaped median face contributing to the foremost part of the lateral wall of the mid-ventral groove; a concave ventral face merging into the dorsal part of the semi-elliptical depression; and a lateral face, separated from the lower third of the anterior ossicular margin by the short groove connecting the triangular facet to the semi-elliptical depression.

The ossicular mid-ventral groove (clg; Text-fig. 19B) probably housed the notochord in life. A poorly preserved, ribbon-like structure visible along the groove is interpreted tentatively as a trace of the dorsal nerve chord. Two narrower grooves project laterally from the ribbon-like structure and end in two pits. Grooves and pits are interpreted tentatively as traces of nerves and ganglia (tsg and tsn; Text-fig. 19B) respectively.

The posterior ossicular surface bears two triangular platforms (tp; Text-fig. 18B) that fit into the triangular depressions of the anterior face of the successive posterior ossicle. A posterior interossicular groove (pig; Text-fig. 18B) is visible in the middle of a posterior oval depression (pod; Text-fig. 18B). Ventro-lateral to each triangular platform is a rounded area (rd; Text-fig. 18B), which accommodates the dorsal arm of the articulation boss of the succeeding ossicle. The uppermost part of the posterior ossicular surface is flat (pbs; Text-fig. 18B). A protuberance (pp; Text-fig. 18B) on the lower third of the posterior margin fits into a notch (dn; Text-fig. 18A) on the anterior margin of the succeeding ossicle (Pl. 7, fig. 9; Pl. 8, figs 3, 5–6, 8).

The ventral ossicular margins are triangular in cross section and are articulated with the dorsal margins of the hind-tail plates. The rearmost part of the ventral ossicular margin bears a facet for the articulation of the successive posterior ventral plate (afvp; Text-figs 18B, 19).

Internal anatomy of the head

Dorsal steinkern (Text-figs 12A, 13A, 14, 15A). The dorsal steinkern carries an oblique groove which runs from its anterior right to its posterior left and divides it into two unequal areas. The groove is asymmetrical in cross section along most of its length, being steeper to the right than to the left. The posterior two-thirds of the groove (ppog; Text-fig. 21A; Text-figs 13–14, 15A), almost straight and asymmetrical in cross section, runs from the posterior left angle of the head to a mid-dorsal pit (mdp; Text-fig. 21A). Before reaching it, the groove deepens and widens. The anterior third (apog; Text-fig. 21A) of the groove runs from the mid-dorsal pit to the right anterior angle of the upper lip. In front of the pit the groove turns sharply rightward and becomes shallower and more symmetrical in section. Before joining the right angle of the upper lip, the groove becomes convex rightward and somewhat deeper again.

Detailed comparisons between mitrates and extant chordates (especially tunicates) are crucial for the interpretation of the internal anatomy of the mitrate head. According to Jefferies (1986), the oblique groove marks the right boundary of the region where the left anterior coelom (left mandibular somite of vertebrates) was in contact with the dorsal head skeleton. The left anterior coelom would overlie the left pharynx.

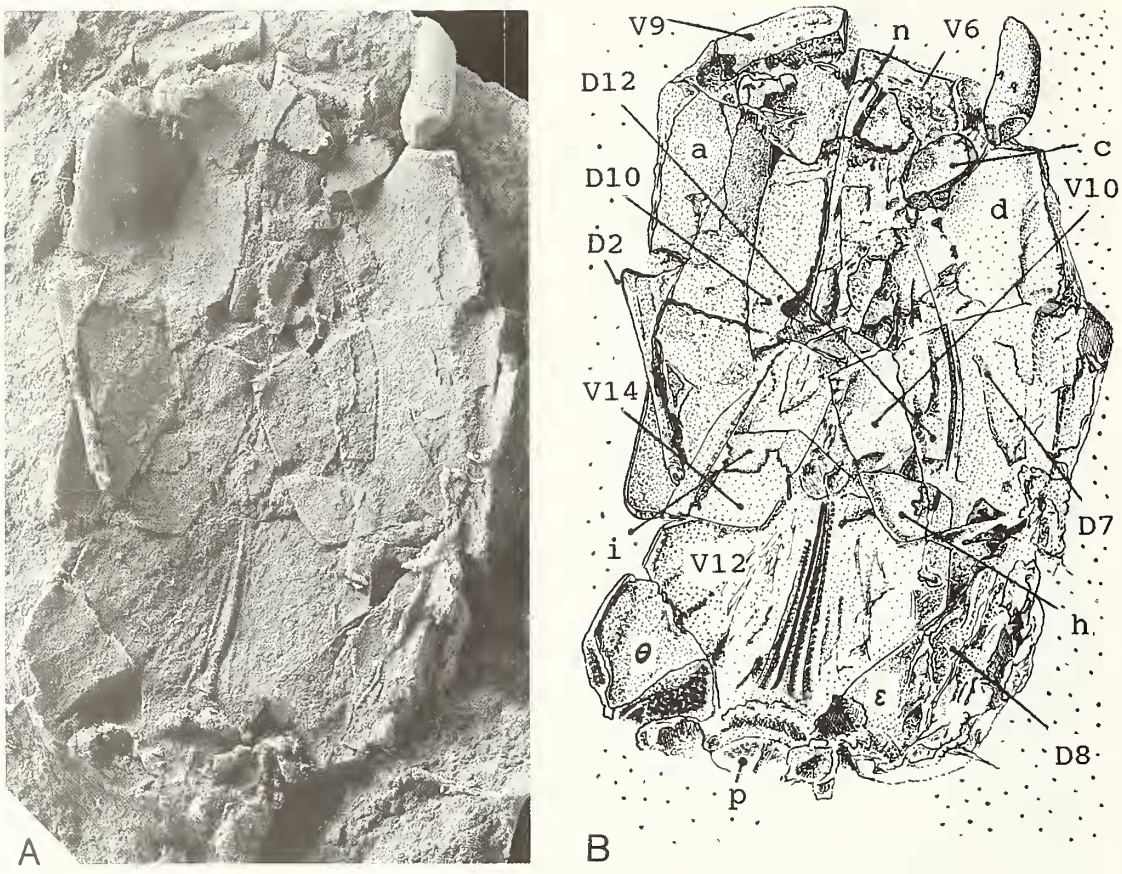
An elongate band (dl; Text-fig. 21A) runs obliquely and posteriorly from the mid-dorsal pit (Text-fig. 13A). It presumably represents the impression of the cavity of the dorsal lamina (Jefferies 1986, pp. 93, 270, 279), a fold of tissue which occupies the mid-dorsal line of the pharynx in some tunicates. In *Mitrocystella incipiens*, the position of the dorsal lamina is marked by two parallel lines on the dorsal steinkern (Jefferies and Lewis 1978; Chauvel 1981; Jefferies 1986), whereas in *P. africana* these lines are irregular. A faint line on the steinkern of h (Text-fig. 13A) would correspond to the left boundary of the right pharynx (lbrp; Text-fig. 21A).

Following Jefferies (1986), the area of the dorsal steinkern right of the impression left by the dorsal lamina corresponds in position to the rightmost part of the right anterior coelom (right mandibular somite of vertebrates), which would overlie the right pharynx in life. Most of the viscera were probably housed below the triangular area comprised between the posterior two-thirds of the oblique groove and the left boundary of the right pharynx.

Two small grooves (rag and rpg; Text-fig. 21A; see also Text-fig. 13A) are visible to the right of and anterior to the right pyriform body in one individual. They may represent a partial right peripheral canal. In other mitrates (e. g. *Mitrocystites mitra*), the left and right peripheral canals are visible along the inner sides of the marginal dorsal plates and would have housed the nerves labelled as n2 (see below).

Another groove is visible in the left postero-lateral region of the dorsal steinkern (lg; Text-fig. 21A). Anterior to this groove, a short ridge (r; Text-fig. 21A) bends downward and slightly medianward, running along the posterior surface of the head steinkern. Comparison with *M. incipiens* suggests that this ridge may represent part of the rectum. The specimen in Text-figure 13A shows the position of the ascending part of the rectum, left of the rearmost part of the oblique groove. The rectum would open into a left atrium, according to Jefferies (1986; see also Jefferies and Lewis 1978). However, the position of the anterior boundary of the left atrium in *P. africana* is unknown. A bump in front of the rag and rpg grooves (see Text-fig. 21A) is interpreted tentatively as a trace of the anterior boundary of the right atrium (abra; Text-fig. 21A).

A crescent-shaped line in front of the posterior margin of the dorsal steinkern (abpc; Text-fig. 21A; Text-figs 13, 14A) corresponds to the anterior wall of the posterior coelom. According to Jefferies (1986), the latter would be homologous with the tunicate epicardia.



TEXT-FIG. 11. *Placocystella africana* (Reed, 1925). A, latex cast of SAM 0101; locality K, Klipfontein; Ceres Subgroup, Voorstehoek Shale; partial dorsal head skeleton, partial dorsal aspect of the ventral head skeleton, endostylar trace, oral spine insertions and anterior margin of ventral head skeleton; ×5; B, interpretative sketch.

EXPLANATION OF PLATE 5

Figs 1–6. *Placocystella africana* (Reed, 1925). Specimen in fig. 1 from Swaarmoed Pass, Ceres; Ceres Subgroup, Voorstehoek Shale; specimens in figs 2, 4 and 6 from locality A, Klipfontein; Ceres Subgroup, Voorstehoek Shale; specimen in fig. 5 from locality K, Klipfontein; Ceres Subgroup, Voorstehoek Shale; specimen in fig. 3 from locality D, Gydopas; Ceres Subgroup, Gydo Shale. 1, latex cast of SAM 0112, anterior aspect of the styloid; note the radial thickenings on the anterior blade and the pit on the dorsal surface of the antero-ventral excavation; ×12. 2, SAM 0107, natural external mould of V12; the impression left by the endostylar trace is visible; ×5. 3, latex cast of SAM 0061, a young individual showing a faint suture between V12 and p; note the distribution of ribs and riblets and the transverse keel on ε; ×5. 4, latex cast of SAM 0013, with ε, p, θ and V12 articulated; riblets and concentric growth lines are visible; ×4. 5, latex cast of SAM 0092, showing the differences in the kind and distribution of ornament on the posterior third of the ventral head skeleton and growth lines; note the finely granular stereom texture of the external surface of V12; ×6. 6, latex cast of SAM 0106, showing the morphology of the right oral spine, its articulation with d, the anterior margin of V6 and the depression lying to the right of the spine articulation on the dorsal surface of V6; ×12.

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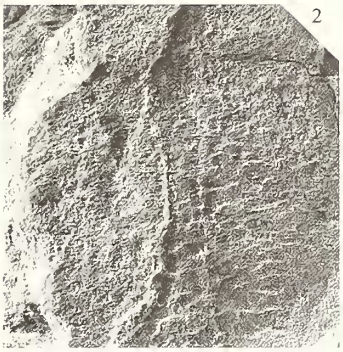
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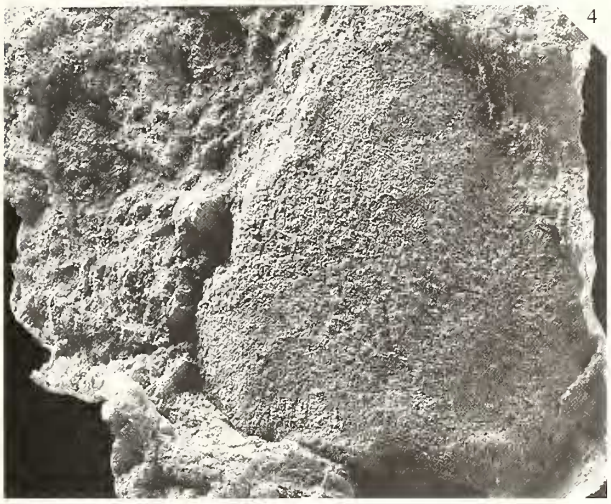
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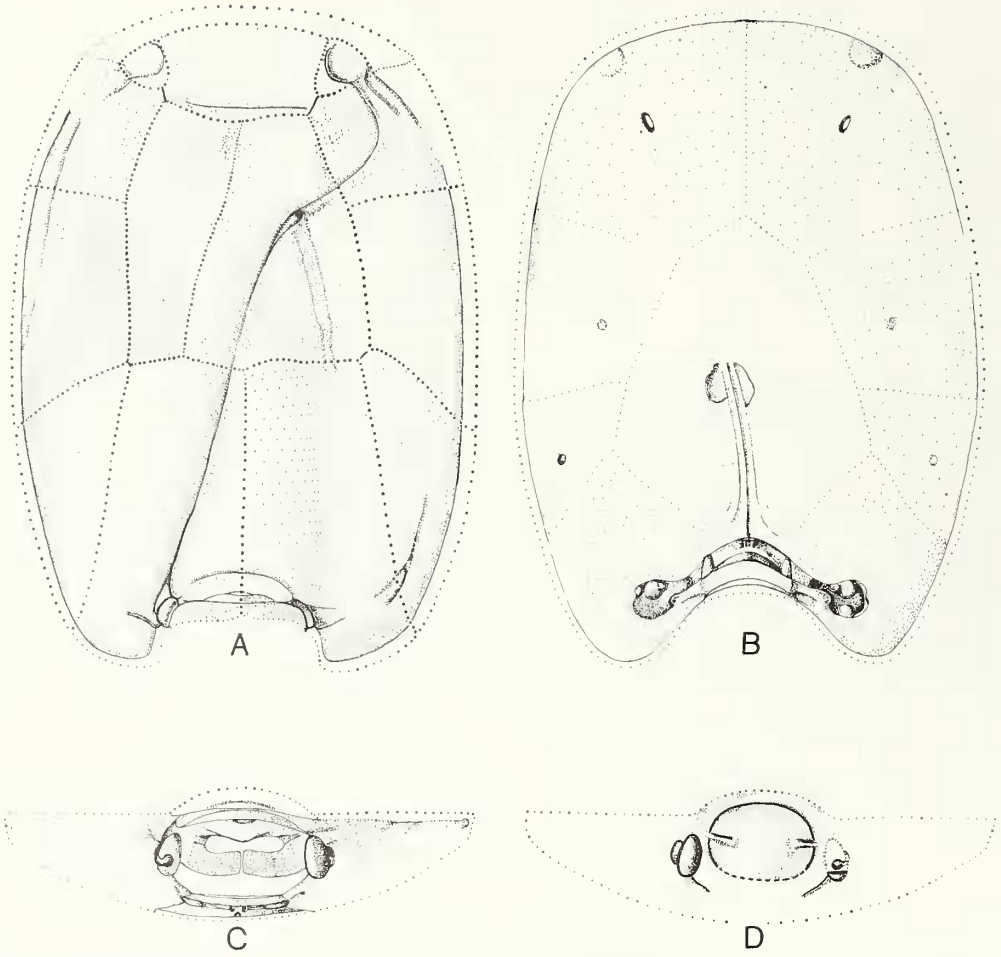
RUTA and THERON, *Placocystella*

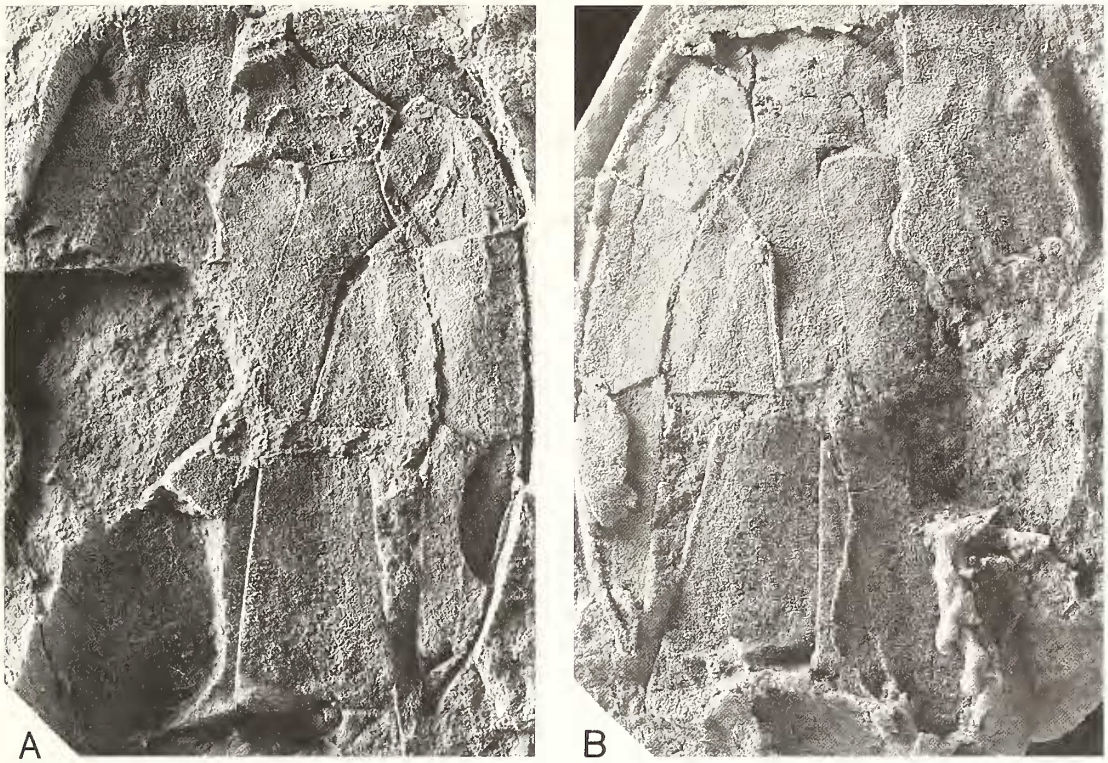


TEXT-FIG. 12. *Placocystella africana* (Reed, 1925). Reconstruction of the internal aspect of the head. A, dorsal view; B, ventral view; C, posterior view; D, anterior view (soft parts of the head removed; left pyriform body drawn in part to show the left acoustic ganglion).

The enlarged, deep part of the oblique groove behind the mid-dorsal pit probably represents, by comparison with *Placocystites forbesianus*, the site of the ciliated organ (opening of the neural gland duct). The pit is the point from which a mid-dorsal process (part of which is visible as a short stump in Text-fig. 13B) would extend inward and rearward to stiffen the free edge of the dorsal lamina (Jefferies and Lewis 1978; Jefferies 1986).

The anteriormost region of the dorsal steinkern shows two bumps (loc and roc; Text-fig. 21A) underneath plates b and c. These are interpreted as olfactory cups on the basis of their position inside the mouth. A faint transverse groove just in front of the posterior margin of n (Text-fig. 13A) may represent the impression of the velum (vg; Text-fig. 21A). The likely position of the head chambers is shown in Text-figure 21A.

Ventral steinkern (Text-fig. 12B; Pl. 7, fig. 1). A groove runs from in front of the p/V12 suture to a point slightly right of the plane of bilateral symmetry. If the interpretation of the internal anatomy of the mitrate head and the dorso-ventral orientation of *P. africana* are correct, it is reasonable to interpret this groove as a trace of the skeletal support for the endostyle (et; Text-fig. 21A), for the groove is mid-ventral in position and the only



TEXT-FIG. 13. *Placocystella africana* (Reed, 1925). A, partial dorsal head steinkern of BMNH EE 5649 (JJS2); Swaarmoed Pass; Ceres Subgroup, Voorstehoek Shale; oblique groove, mid-dorsal pit, velar groove, foremost part of dorsal lamina, right boundary of left pharynx, anterior boundary of right atrium, right olfactory organ and partial course of the right nerve n2. B, latex cast of the same specimen, showing the position of the rectum and of the anterior boundary of the left atrium; both × 5.

important mid-ventral organ in the pharynx of primitive living chordates is the endostylar gland (Jefferies 1986). The endostylar trace is V-shaped in cross section and slightly convex leftward in most specimens, although variation exists (Text-fig. 11). It stops posteriorly in front of a transverse excavation extending between the pyriform bodies (see below) and is flanked on both sides by a fainter, lateral groove (Pl. 7, fig. 1). The latter runs parallel to the endostylar groove for most of its length, but diverges outward posteriorly. Another faint line, visible on both sides of the endostylar trace (Pl. 7, fig. 1), runs parallel to the endostylar and lateral groove, but is shorter. The steinkern of V12 has a dappled aspect and shows concentric growth lines.

Allanicytidium flemingi from New Zealand (Caster and Gill 1967, fig. 361; Caster 1983, fig. 1) shows a similar presumed ventral endostylar trace (er; Text-fig. 22). This is concave leftward and runs from in front of the p/V12 suture to slightly right of the centre of V12, where it turns leftward. A depression on both sides of the endostylar ridge follows the curvature of the latter. The left depression (ld; Text-fig. 22) is deeper than the right one for most of its length, but becomes shallower anteriorly. Left of this depression, the dorsal surface of V12 shows two triangular areas (tsa1 and tsa2; Text-fig. 22) surrounded by a faint, tortuous crest (lfc; Text-fig. 22). The crest delimits three other depressions laterally (tsd1, tsd2 and tsd3: Text-fig. 22), continues anteriorly for a short distance flanking the endostylar ridge, and disappears before the latter changes direction. The depression on the right of the endostylar ridge (rd; Text-fig. 22) is flanked by another crest (rfc; Text-fig. 22). A transversely elongate pit (ep; Text-fig. 22) lies anterior to the endostylar ridge. The dappled aspect of V12 in *P. africana* and the depressions and ridges on both sides of the endostylar ridge in *A. flemingi* are difficult to interpret; possibilities are blood vessels, nerves, or viscera.

By combining information from different specimens it is possible to detect the existence of three sub-circular depressions on the ventral steinkern of *P. africana*, corresponding to central buttons on the dorsal surface of

some ventral plates (Text-fig. 14; Pl. 2, fig. 3). The likely existence of three other buttons is deduced from a comparison with *A. flemingi*. The buttons are remnants of the inner calcitic layer of the three-layered ventral skeleton typical of all mitrates. Their function is unknown. Two asymmetrical buttons in front of the endostylar trace in one specimen (Pl. 7, fig. 7) resemble similar structures in *Barrandeocarpus norvegicus* (Craske and Jefferies 1989, figs 14b, 17; pl. 13, fig. 2).

A depression on the anterior margin of V6 and V9 (Text-figs 9, 11; Pl. 1, fig. 2; Pl. 4, fig. 3; Pl. 5, fig. 6) may represent the external opening of an inlet valve or a continuation of the olfactory organs.

Nervous system

According to the calcichordate interpretation of mitrates, the inflated structure at the head/tail junction is the brain, divided into prosencephalon and deuterencephalon (pros and deut; Text-fig. 16; Pl. 4, fig. 6; Pl. 7, figs 2–3). As in *Placocystites forbesianus*, the prosencephalon of *P. africana* is lens-shaped, but with no obvious distinction between telencephalon and diencephalon. The deuterencephalon is less expanded transversely than in *P. forbesianus*.

Two hypocerebral processes (hyp; Text-fig. 16), almost in contact medially, delimit a transverse optic foramen (of; Text-fig. 16; Pl. 4, fig. 6; Pl. 7, fig. 6). In one individual (Pl. 7, fig. 6), a ridge projecting upward from the right half of the foramen probably represents the right cispharyngeal optic nerve. A left cispharyngeal optic nerve has not been observed. Above the foramen is a thick crescentic body (premandibular somite of vertebrates; Jefferies 1986, fig. 8.23).

The postero-ventral head steinkern is reconstructed in Text-figure 20, based on specimen BMNH EE 5653 (JJS6; Pl. 7, figs 1, 7). The groove extending laterally out to each of the two pyriform bodies corresponds to a skeletal wall behind the p/V12 suture. The upper edge of this wall is blunt. Its posterior surface is convex, whereas its anterior surface is concave. The latter marked the anterior boundary of the posterior coelom ventrally.

Two ridges (n0; Text-fig. 20; Pl. 7, fig. 1), visible on the anterior face of the transverse groove on the postero-ventral steinkern, are probably traces of the nerves n0, present in *Placocystites forbesianus*, *Barrandeocarpus norvegicus* and *Eunitrocystella savilli*. These nerves are believed to have supplied the endostyle in life on the basis of their position on the internal surface of the ventral head skeleton (Jefferies and Lewis 1978; Jefferies 1986, p. 278). The fact that the nerves n0 in *P. africana* are visible as ridges on the steinkern suggests that the transverse wall behind the endostylar ridge (Pl. 7, fig. 7) was formed in life entirely of the outer calcitic layer. In *Mitrocystella incipiens* and *P. forbesianus*, this region is formed of the inner calcitic layer and the nerves run between the outer and the inner layers.

The thickenings labelled as bpc in Text-figure 20 may represent the median, lower parts of the two palmar complexes. In other mitrates, these structures give rise to various nerves. With the exception of nerves n2, the other nervous branches are not observed in *P. africana*. Nerves n2 (Text-fig. 21A), regarded by Jefferies (1986) as homologous with the maxillary branches of the trigeminal nerves, are partially preserved as ridges on the lateral walls of the steinkern and terminate in the buccal cavity, lateral to the olfactory cups (Text-figs 13, 14B).

The pyriform bodies (trigeminal ganglia in Jefferies' view) are antero-lateral to the deuterencephalon (Text-figs 12, 13A, 15B, 20; Pl. 7, fig. 1), but their median connections are unknown. Their major axis is inclined antero-medially. A small lump and a slender ridge visible near the left pyriform body are tentatively interpreted as a left auditory ganglion and a left acoustic nerve respectively (lag and lan; Text-fig. 20; Pl, 7, fig. 1; see Cripps (1990) for the interpreatation of similar structures in the mitrate *Chaubelia discoidalis*). A small raised lump right of the right pyriform body (Text-figs 13, 15B) is tentatively interpreted as the right auditory ganglion.

EXPLANATION OF PLATE 6

Figs 1–6. *Placocystella africana* (Reed, 1925). Specimens in figs 1–4 and 6 from Swaarmoed Pass, Ceres; Ceres Subgroup, Voorstehoek Shale; specimen in fig. 5 from locality A, Klipfontein; Ceres Subgroup, Voorstehoek Shale. 1, 3, latex casts of part and counterpart of BMNH EE 5656 (JJS9): 1, fore-tail rings (left part of the photograph), styloid (centre) and hind-tail ossicles (right part of the photograph); 3, isolated ossicles (left part of the photograph). 2, 4, part and counterpart of BMNH EE 5662 (JJS15), fore-tail rings: 2, natural ventral external mould of part; 4, latex cast of dorsal extenal mould of counterpart. 5, latex cast of SAM 0011, dorsal head skeleton, oral spines and fore-tail rings and partially disrupted styloid. 6, latex cast of SAM 0112, articulation facets of oral spine and anterior aspect of the styloid. All ×5.

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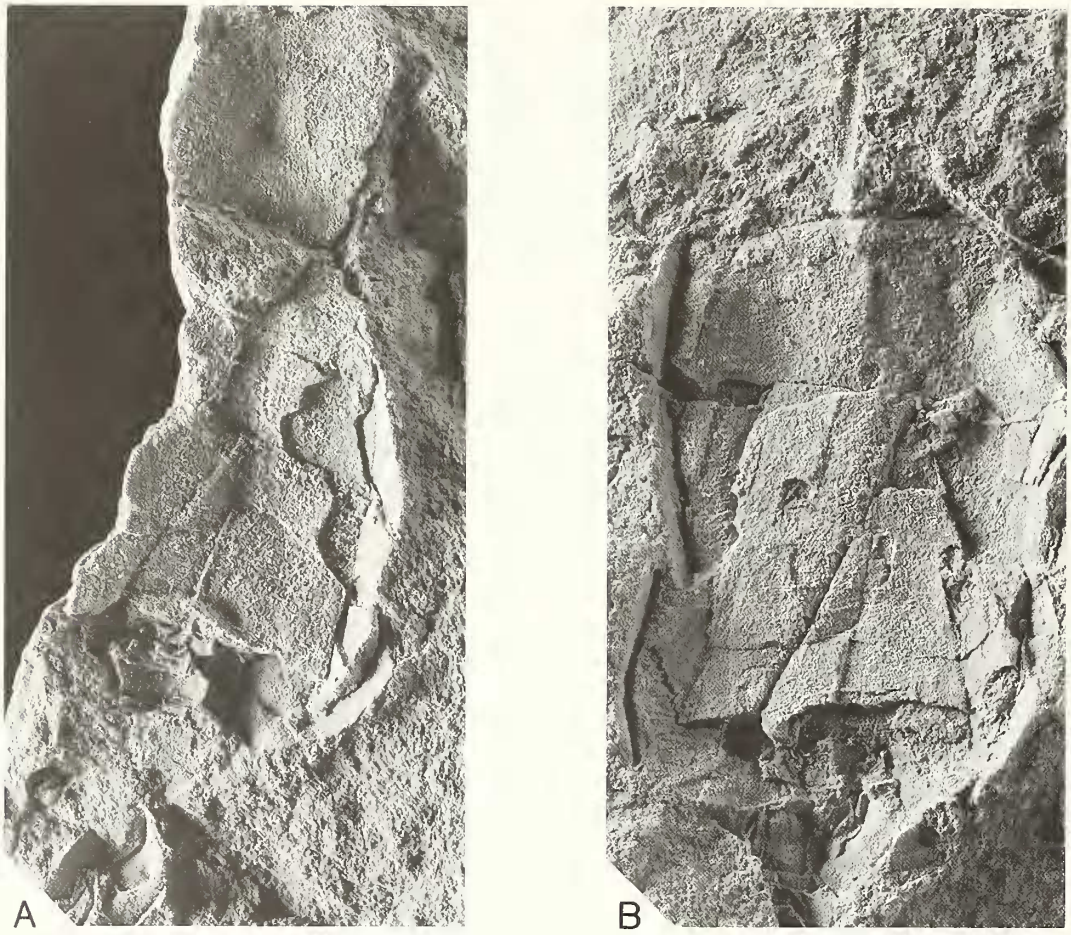
RUTA and THERON, *Placocystella*



TEXT-FIG. 14. *Placocystella africana* (Reed, 1925). A, partial dorsal and ventral head steinkerns of SAM 0009; locality A, Klipfontein; Ceres Subgroup, Voorstehoek Shale; anterior boundary of posterior coelom, rearmost part of oblique groove and left boundary of right pharynx; a depression is visible on the steinkern of V6; ×6. B, partial dorsal and ventral head steinkerns of BMNH EE 5654 (JJS7); Swaarmoed Pass; Ceres Subgroup, Voorstehoek Shale; a depression on the steinkern of V9 and the partial course of the left nerve n2 are visible; external moulds of the oral spines preserved; ×6.

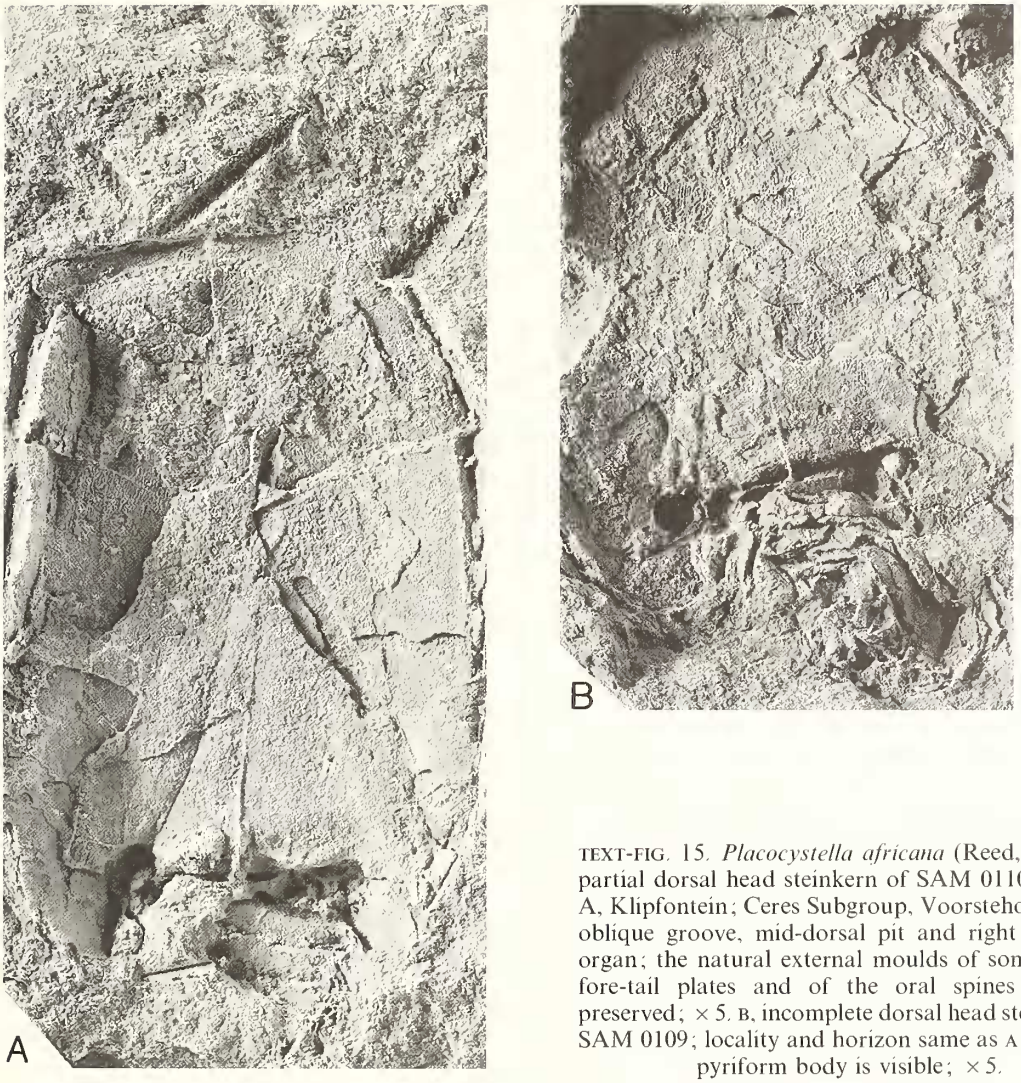
Family *Incertae sedis*

Genus BOKKEVELDIA gen. nov.

Derivation of name. From the Bokkeveld Group of South Africa.

Type species. Bokkeveldia oostluizeni sp. nov., the only known species.

Diagnosis. Five transverse rows of ventral plates; first, third and fourth row with five plates each; second and fifth row with four and three plates respectively; V11 and V13 smaller than V7, V8, V16 and V18; V17 contacts p, V12, V16 and V18; V12 separated from V3 by V7 and V8; ε separated from θ by p; ribs on V15, V16, V18, V19, ε, p and θ.



TEXT-FIG. 15. *Placocystella africana* (Reed, 1925). A, partial dorsal head steinkern of SAM 0110; locality A, Klipfontein; Ceres Subgroup, Voorstehoek Shale; oblique groove, mid-dorsal pit and right olfactory organ; the natural external moulds of some ventral fore-tail plates and of the oral spines are also preserved; ×5. B, incomplete dorsal head steinkern of SAM 0109; locality and horizon same as A; the right pyriform body is visible; ×5.

Bokkeveldia oosthuizeni gen. et sp. nov.

Text-figure 6A–B

1984 *Placocystella* sp. (a) Rennie; Oosthuizen, p. 134, table 3.

Derivation of name. After Mr R. D. F. Oosthuizen of Zwartskraal, Cape Province, discoverer of the holotype, for his contributions to the biostratigraphy and palaeontology of the Bokkeveld Group.

Material. Complete external mould of a ventral head skeleton slightly disrupted in the posterior part. The specimen (Oosthuizen's collection, no. 148) was legally bequeathed to the South African Museum, Cape Town.

Type locality and horizon. Gamka Poort, Prince Albert Area, Gydo Shale; 33°18′S, 21°38′E.

Diagnosis. As for the genus, by monotypy.

Remarks. Although known from poor material, *Bokkeveldia oosthuizeni* shows a remarkable morphology. Its ventral plate arrangement is here chosen as a reference to identify homologous plates in all the mitrates with a standardized ventral head skeleton. In the vast majority of the anomalocystitids, the ventral head skeleton consists of a fixed number of plates arranged in transverse rows. The plates can be subdivided topographically in mid-ventral, admedian ventral and lateral ventral elements. A comparison with *Bokkeveldia* makes it possible to assign a particular plate to one or the other of these three spatial groups. The identification of homologous plates in the anomalocystitids will be dealt with extensively elsewhere.

Bokkeveldia oosthuizeni is similar to an unnamed lower Devonian mitrate from Morocco described and figured by Regnault and Chauvel (1987, fig. 1) and known from a single individual (specimen IGR 16639, Institut de Géologie, University of Rennes, France) of which the head steinkern and part of the dorsal skeleton are known. The ventral steinkern of the Moroccan mitrate bears the impressions of polygonal plates arranged in at least four transverse rows, but the incomplete preservation of this fossil makes it difficult to draw more accurate comparisons with *Bokkeveldia*.

PHYLOGENETIC ANALYSIS

Thirteen taxa were chosen for this study: *Allanicytidium flemingi* Caster and Gill (Reefton Mudstone, New Zealand), *Ateleocystites guttenbergensis* Kolata and Jollie (Guttenberg Formation, Wisconsin, USA), *Australocystis langei* Caster (Ponta Grossa Shale, Brazil), *Barrandeocarpus jaekeli* Ubaghs (Letná Formation, Czech Republic), *B. norvegicus* Craske and Jefferies (Langøyene Sandstone, Norway), *Eumitrocystella savilli* Beisswenger (Ouine-Inirne Formation, Morocco), *Mitrocystella barrandei* Jaekel (Šárka Formation, Czech Republic), *M. incipiens* (Barrande) (Dobrotivá Formation, Czech Republic, and Formation de Traveusot, France), *Notocarpos garratti* Philip (Humevale Formation, Victoria, Australia), *Placocystella africana* (Reed) (Gydo and Voorstehoek shales, South Africa), *Placocystites forbesianus* de Koninck (Wenlock Limestone, England), *Tasmanicytidium burretti* Caster (Richea Siltstone, Tasmania, Australia) and *Victoriacystis wilkinsi* Gill and Caster (Dargile Beds, Victoria, Australia).

The morphological data are gleaned mainly from the works of Caster (1954, 1983), Gill and Caster (1960), Caster and Gill (1967), Ubaghs (1967, 1979), Jefferies and Lewis (1978), Chauvel (1981), Philip (1981), Kolata and Jollie (1982), Jefferies (1986), Craske and Jefferies (1989), Parsley (1991) and Beisswenger (1994).

All characters were left unweighted and unordered and processed with PAUP 3.1.1 (Swofford 1993) under the ACCTRAN optimization, which explains homoplasy in terms of reversals. One

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EXPLANATION OF PLATE 7

Figs 1–9. *Placocystella africana* (Reed, 1925). Specimens in figs 1–3, 7 from Swaarmoed Pass, Ceres; Ceres Subgroup, Voorstehoek Shale; specimens in figs 5–6 from locality K, Klipfontein; Ceres Subgroup, Voorstehoek Shale; specimens in figs 4 and 8 from locality A, Klipfontein; Ceres Subgroup, Voorstehoek Shale; specimen in fig. 9 from locality J, Lakenvalleidam; Ceres Subgroup, Voorstehoek Shale. 1, 7, BMNH EE 5653 (JJS6) and latex cast; left pyriform body, left acoustic nerve and left auditory ganglion; note the endostylar groove, flanked on both sides by two fainter grooves, and the dappled aspect of the steinkern of V12; growth lines and two asymmetrical 'buttons' visible in front of the endostylar trace; × 5. 2–3, BMNH EE 5654 (JJS7), showing the brain: 2, dorsal view; 3, anterior view; × 5. 4, latex cast of SAM 0013, endostylar trace and partially eroded lower cups of pyriform bodies; × 5. 5, latex cast of SAM 0132, endostylar ridge and adjacent ridges; × 6. 6, SAM 0050, head steinkern in posterior view, optic foramen and right cyspharyngeal optic nerve running laterally from the right half of the foramen; × 5. 8, SAM 0109, rearmost part of internal surface of dorsal head skeleton with the impression of the anterior boundary of the posterior coelom and part of the brain; × 5. 9, latex cast of SAM 0139, mid- and hind-tail in right lateral view; × 7.

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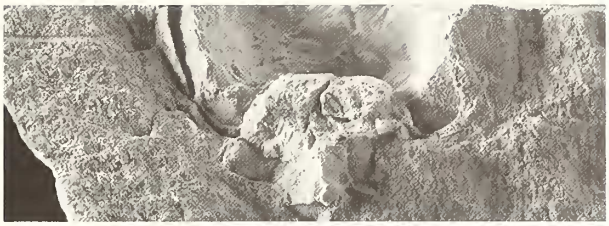

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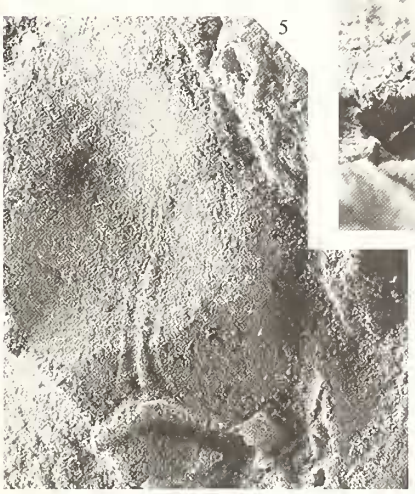

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RUTA and THERON, *Placocystella*

parsimonious tree (branch-and-bound algorithm; length = 51; CI = 0·857 excluding uninformative characters nos 27 and 35; RI = 0·929) was found. *Mitrocystella barrandei* and *M. incipiens* were used as outgroups. In *Australocystis*, the multi-state coding for character no. 16 (2 or 3) means uncertainty. The analysis was subject to bootstrap, which estimates the support of a hypothesis of phylogeny (in our case based on parsimony) through repeated sampling of characters, regardless of the historical reality of a clade (Hillis and Bull 1993). The 50 per cent. majority-rule consensus tree (Text-fig. 25; 1000 replicates; branch-and-bound search) shows high bootstrap values at nodes D (100 per cent.), I (100 per cent.) and E (97 per cent.), intermediate values at F (88 per cent.), C (85 per cent.) and J (83 per cent.) and low values at H (70 per cent.), L (63 per cent.) and K (50 per cent.).

Node F is supported by three character-state changes: 9 refers to the regular ventral plating pattern; 22 refers to the presence of oral spines (their insertions are visible in *Ateleocystites* and *Allanicytidium*); 16 refers to the differentiation of V12 which in *Ateleocystites* occupies the second ventral row and extends anteriorly and posteriorly to separate in part the admedian plates of the first and third row respectively.

Node G is supported by character-state changes nos 13, 16 and 24. Character no. 13 concerns the absence of admedian elements in the third ventral row. Reversal is found in *Victoriacystis*, in which two small plates seem to be present postero-lateral to the large mid-ventral plate (Gill and Caster 1960, fig. 11b; pl. 9, fig. 2; pl. 10, fig. 2). These elements, V11 and V13, are also small in *Bokkeveldia* by comparison with V10 and V14. If the identification of V11 and V13 in *Victoriacystis* is correct, their size may be interpreted as a stage of their progressive reduction in passing from the less derived anomalocystitids to the allanicytidiids, which lack V11 and V13. The absence of V11 and V13 in *Placocystites* may also be interpreted as a parallelism with the Allanicytidiidae (this is evident when the DELTRAN optimization is in effect). Characters nos 16 and 24 concern the expansion of V12 and the absence of D11.

Node H is supported by character-state changes nos 12 (second ventral row formed by two lateral elements), 30 (flexible upper lip) and 31 (lack of oral platelets). The second ventral row is absent in *Placocystites*, as tentatively deduced from the fact that in this mitrate three elements form the anterior row, of which one is mid-ventral. On the basis of their relative position with respect to other plates, these elements are probably homologous with V2–V4 of *Victoriacystis* and *Bokkeveldia*.

The monophyly of the Allanicytidiidae (node I) is supported by ten state changes: 7, 10–11, 14–16 and 23 refer to the arrangement of the ventral plates (preserved only in part in *Australocystis langei*); 3 refers to the styloid blades (poorly preserved in *Australocystis*; unknown in *Tasmanicytidium burretti*); 29 and 32 refer to plates b, n and c. The distribution of dorsal ribs, the general head proportions and the shape of D10 and D12 are similar in *Notocarpos garratti* and in *Placocystites forbesianus*. Node J is supported by the presence of ventral riblets (21; unknown state at node L) and by the rearward extension of D10 (33). *P. africana* is the sister taxon of *Allanicytidium* plus *Australocystis* (node K; character no. 37, presence of dorsal riblets). *Allanicytidium* and *Australocystis* (node L) share the similar shape of D10 and D12 (34).

EXPLANATION OF PLATE 8

Figs 1–9. *Placocystella africana* (Reed, 1925). Specimens in figs 1, 3–5 and 7 from Swaarmoed Pass, Ceres; Ceres Subgroup, Voorstehoek Shale; specimen in fig. 2 from locality A, Klipfontein; Ceres Subgroup, Voorstehoek Shale; specimens in figs 6 and 8 from locality D, Gydopas; Ceres Subgroup, Gydo Shale. 1, 9 BMNH EE 5662 (JJS15): 1, natural mould of styloid; × 10; 9, latex cast of styloid in antero-lateral view; × 7. 2, latex cast of SAM 0014, latero-ventral aspect of the head; the hind-tail is bent under the head; × 5. 3, latex cast of BMNH EE 5658 (JJS11), isolated hind-tail ossicles; × 5. 4, latex cast of of SAM 0114, fore-tail rings surrounding the anterior styloid process; × 5. 5, latex cast of BMNH EE 5656 (JJS9), isolated hind-tail ossicle in anterior view; × 12. 6, 8, part and counterpart of SAM 0104, external mould of the hind-tail; note the ossicular articulations; × 5. 7, specimen BMNH EE 5662 (JJS15), natural mould of posterior ossicular surface; × 10.

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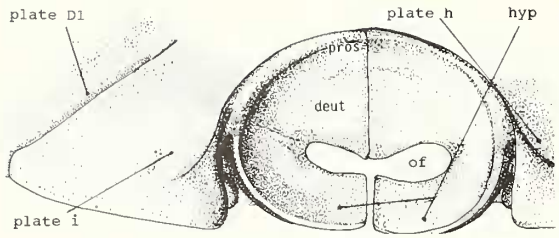
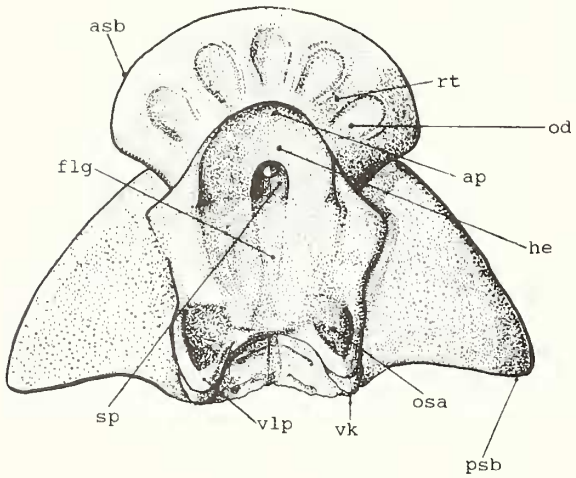
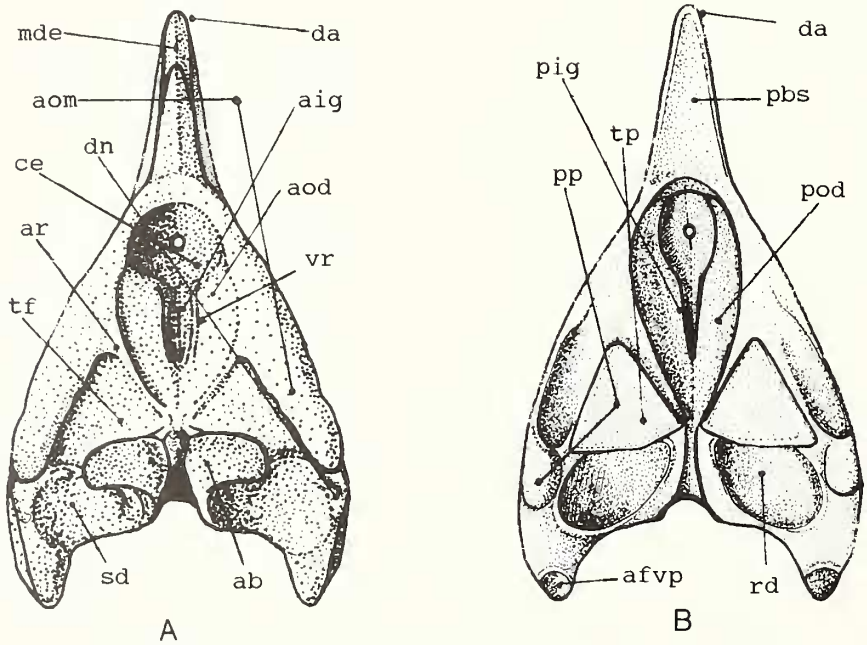


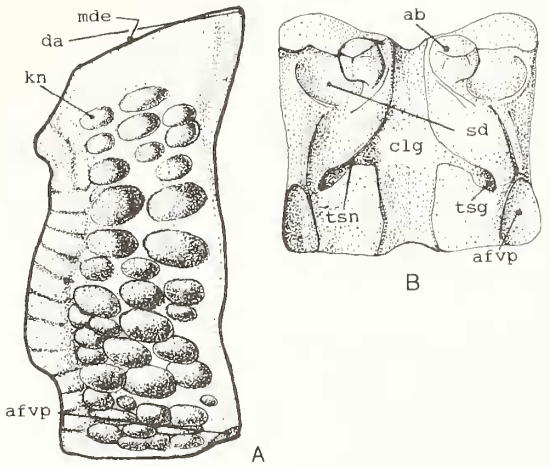
TEXT-FIG. 16. *Placocystella africana* (Reed, 1925). Reconstruction of the posterior head skeleton, showing the two hypocerebral processes, the optic foramen and the division of the cerebral basin into a prosencephalar and a deuterencephalar part. Abbreviations as in the text.



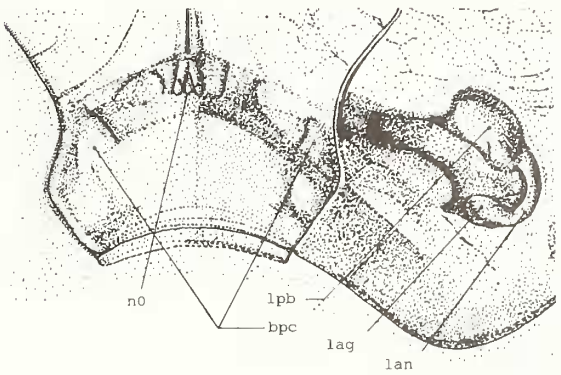
TEXT-FIG. 17. *Placocystella africana* (Reed, 1925). Reconstruction of the styloid in antero-ventral view. Abbreviations as in the text.



TEXT-FIG. 18. *Placocystella africana* (Reed, 1925). Reconstruction of a tail ossicle. A, anterior view; B, posterior view. Abbreviations as in the text.



TEXT-FIG. 19. *Placocystella africana* (Reed, 1925). Reconstruction of a tail ossicle. A, left view; B, ventral view. Abbreviations as in the text.

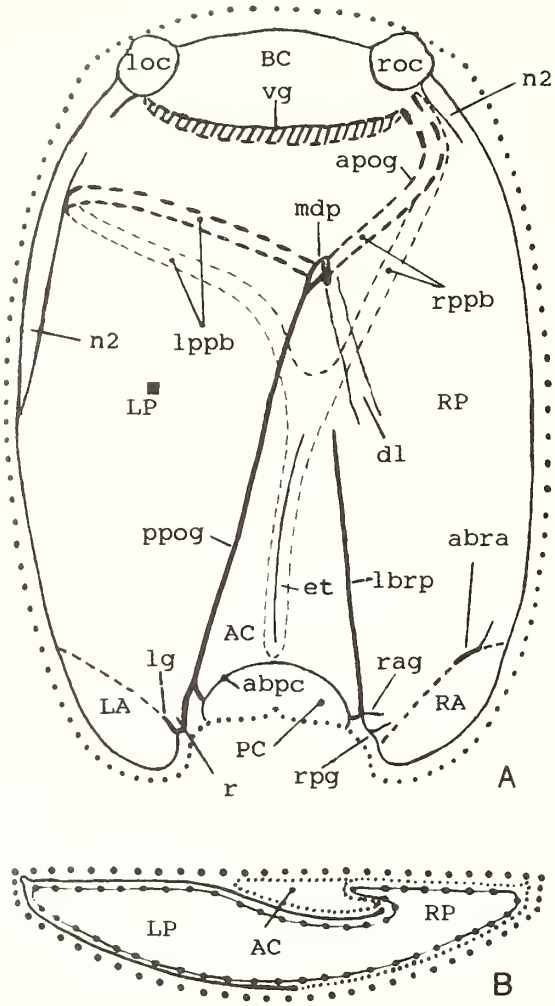


TEXT-FIG. 20. *Placocystella africana* (Reed, 1925). Reconstruction of the postero-ventral head steinkern. Abbreviations as in the text.

Six minimal trees were found when *Bokkeveldia* was included in the analysis. Their strict consensus placed this mitrate with *Ateleocystites*, *Placocystites* and *Victoriacystis* in a polytomy. The monophyly of the Allanicytidiidae was supported in all trees and the relative positions of the other ingroup taxa did not change.

DISCUSSION

The allanicytidiids show a remarkable external bilateral symmetry, also evident in the plate arrangement, and a peculiar ornament. Jefferies (1984, p. 308) showed that in the ontogeny of *Placocystites forbesianus* the first ribs appeared ventrally and '... tended to be short and crescentic, but became elongated, joined together, and straightened as the head grew; at any given stage, therefore, the straightest and most continuous ribs are found in the posterior part of the ribbed area'. The pattern of ornament in the allanicytidiids suggests that, during their evolutionary history, they acquired riblets in the same ontogenetic order of appearance of ribs as observed in *P. forbesianus*. This sequence seems to reflect the phylogenetic order of appearance of ribs. *Mitrocystites mitra* shows few, short ribs along the postero-lateral head margins. *Mitrocystella incipiens* bears postero-ventral ribs. *Barrandeocarpus* spp. and many anomalocystitids possess transverse dorsal ribs. In *Notocarpos*, ventral ribs are confined to the postero-lateral areas of the head floor and become broken medially (Philip 1981, fig. 5c). *Tasmanicytidium* has a smooth dorsal skeleton, but the ventral skeleton is covered with few riblets and the lateral head walls show broken ribs. In *P. africana*, dorsal riblets replace most of the ribs. The few, sinuous dorsal ribs of *P. africana*

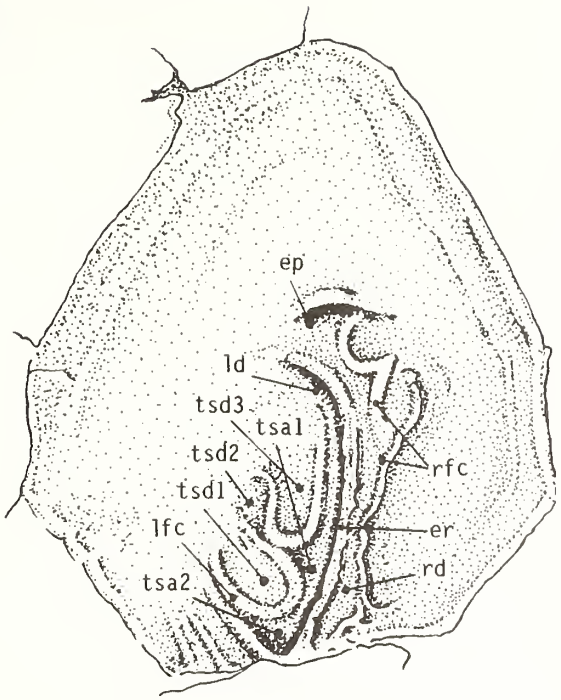


TEXT-FIG. 21. *Placocystella africana* (Reed, 1925). Reconstruction of the chambers of the head. A, dorsal aspect; B, cross section behind the widest point of the head. Abbreviations: AC, patent part of right anterior coelom; BC, buccal cavity; LA, left atrium; LP, left pharynx; PC, posterior coelom; RA, right atrium; RP, right pharynx. Other abbreviations as in the text. In B the continuous line surrounding the left pharynx is the virtual left anterior coelom; the dotted line surrounding the right pharynx is the virtual part of the right anterior coelom. The peripharyngeal bands (lppb and rppb) are hypothetical.

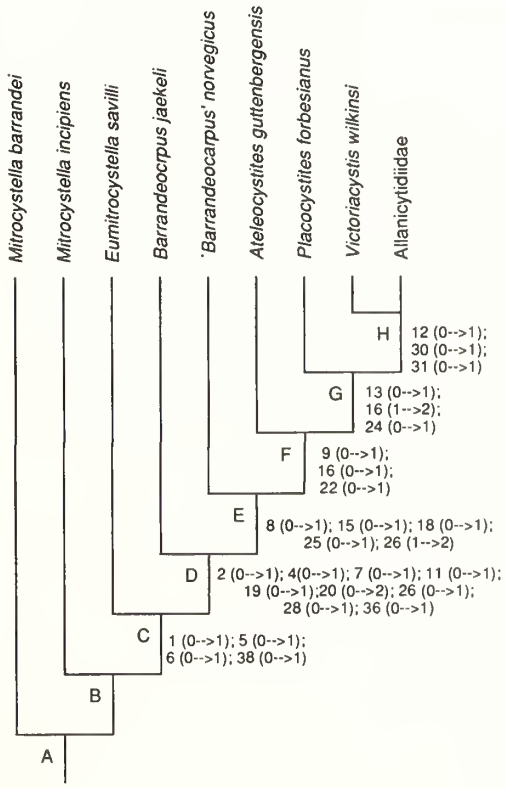
seem to derive from the confluence of riblets. The ventral riblets are more numerous in *Placocystella* than in *Tasmanicytidium*. *Allanicytidium* has numerous dorsal riblets. Few ribs are present near the postero-lateral angles of its head roof. Its ventral ornament is unknown. Changes in the ornament probably occurred through the retention of a juvenile feature (riblets) found in less derived forms.

Australocystis, *Victoriacystis* and *Tasmanicytidium* deserve a final comment. *Australocystis* is certainly an allanicytidiid. The holotype (Caster 1954, fig. 1; pl. 8, figs 1–2) shows a square dorsal elevation, resulting from the post-mortem squashing of the dorsal skeleton against V12 (a condition observed also in some specimens of *P. africana*). V6 and V9 are visible in dorsal view and their anterior margin is asymmetrical in section, as in all other allanicytidiids. Furthermore, the dorsal plating pattern of *Australocystis* is very similar to that of *Allanicytidium*.

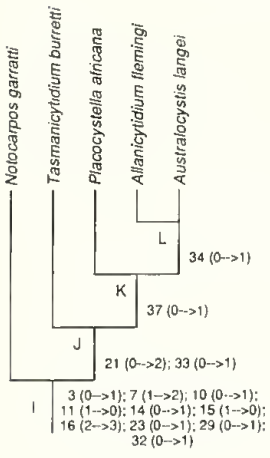
In *Victoriacystis*, a large mid-ventral plate in front of V17 probably contacts anteriorly V2–V4 and may correspond to V12, which incorporated or eliminated V7 and V8. V6 and V9 show the same relative position with respect to the surrounding plates as in *Ateleocystites* and *Bokkeveldia*. The third, fourth and fifth rows in *Victoriacystis* are comparable to those of *Bokkeveldia*, except for the size of V12. The transition from *V. wilkinsi* to *N. garratti* was probably marked by the loss of V1–V5, V11, V13, and V16–V18. Our interpretation of the anatomy of *Victoriacystis* rests on the



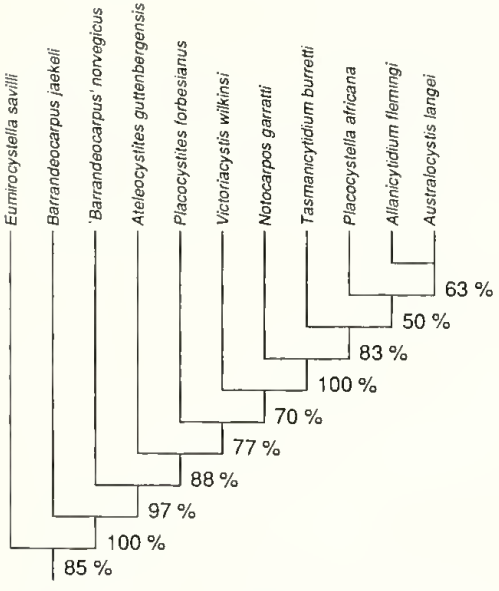
TEXT-FIG. 22. Dorsal aspect of plate V12 in *Allanicytidium flemingi*. Abbreviations explained in the text (redrawn after Caster and Gill 1967).



TEXT-FIG. 23. Cladogram of a selected number of anomalocystitid and mitrocystitid mitrates. Synapomorphies are discussed in the text.



TEXT-FIG. 24. Interrelationships of the Allanicytidiidae. Characters discussed in the text.



TEXT-FIG. 25. Bootstrap 50 per cent. majority-rule consensus tree.

original illustrations in Gill and Caster (1960), and further work on the morphology of this mitrate is necessary.

For Caster (1983, fig. 4), *Tasmanicytidium* had a single centro-dorsal plate and the matrix infilling lying to the right of it represented the area formerly occupied by the admedian half of a marginal plate. However, the marginal plates of this mitrate show no signs of breakage. Perhaps a second centro-dorsal was present in life to the right of the preserved one, suggesting that D10 was wider than D12. An accurate reconstruction of *Tasmanicytidium* depends upon more complete finds.

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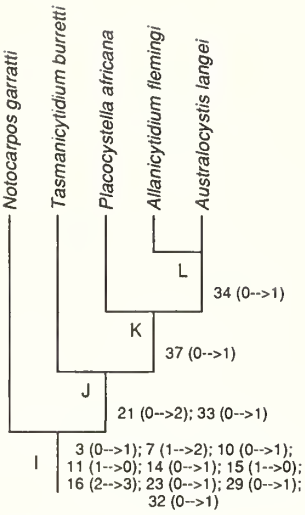

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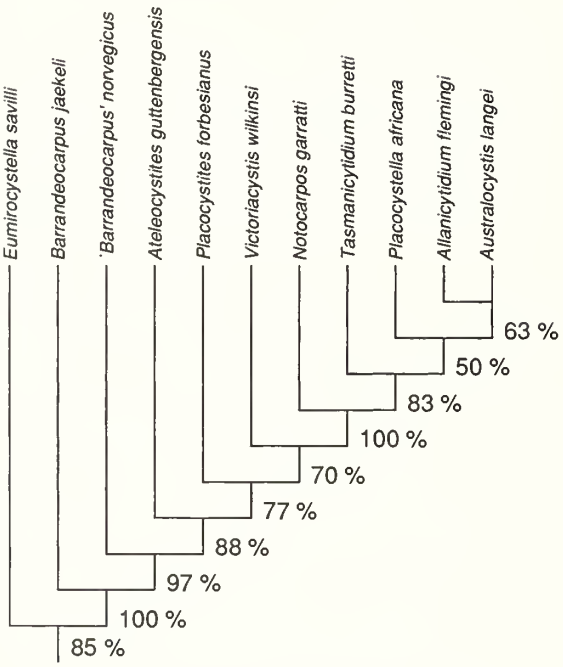

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M. RUTA

Department of Biology
Birkbeck College
Malet Street, London WC1E 7HX, UK
and
Department of Palaeontology
The Natural History Museum
Cromwell Road, London SW7 5BD, UK

J. N. THERON

Geological Survey
P.O. Box 572
Bellville, Cape Town
South Africa

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